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HYBRIDIZATION AND SPECIATION IN *HYALOPHORA* (INSECTA: LEPIDOPTERA: SATURNIIDAE): A REAPPRAISAL OF W. R. SWEADNER'S CLASSIC STUDY OF A HYBRID ZONE

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ABSTRACT

The historical significance of W. R. Sweadner's (1937) classic study of natural hybridization in *Hyalophora* is discussed in terms of contemporary and modern species concepts. Sweadner proposed that *Hyalophora* "*kasloensis*," from the Bitterroot Mountains of the Pacific Northwest, represents a natural hybrid population. In this monograph I re-examine his thesis using experimental hybridization and multivariate analysis, with laboratory hybrids serving as standards of reference. The ecology and immature stages of "*kasloensis*" are described. Biogeographical data, morphology of immature stages, morphometric data, and genetic compatibility in crosses with congeners all independently support the thesis that "*kasloensis*" populations are of hybrid origin. Two other newly discovered hybrid *Hyalophora* populations from the Pacific Northwest are described. Natural hybridization in *Hyalophora* is discussed in terms of various hybrid zone models. The genus *Hyalophora* represents a hierarchy of species, lacking effective prezygotic isolation, but exhibiting varying degrees of postzygotic barriers.

INTRODUCTION

> Nature is lavish in her provision and wasteful in her economy. It is often difficult to tell where her reckless generosity ends and where the delicate limitations for the good of the species begins; in how far the individual shapes the race, or how far natural selection or other agencies eliminate the individuals in unnoticed millions in order to make the species the unit.

From Rau and Rau (1913:245) in introducing their study of fertility and embryo mortality in *Hyalophora cecropia.*

The Monograph by Sweadner

In 1937 Walter R. Sweadner published a monograph on the genus *Hyalophora* Duncan (= *Platysamia*; Lepidoptera: Saturniidae) in which he proposed natural hybridization as the basis for an intergrade population in the Bitterroot Mountains of the Pacific Northwest. He also advocated experimental hybridization as a tool in establishing phylogenetic relationships. This classic monograph appears to be the first comprehensive study published in English of a hybrid zone, a decade after the German classic by Meise (1928), and was the first to use a hybrid index to quantify phenotypic variation. Evolutionary biologists (Dobzhansky, 1951; Mayr, 1963; Dillon, 1973) cited Sweadner's monograph, both for its methods of investigation and for its modern views of the nature of species. However, in the intervening years few people have collected or reared the *Hyalophora* from the Bitterroot region, and the taxonomic status of these supposed hybrid populations

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was uncertain. The name *kasloensis* was placed in synonymy with *H. euryalus* by Ferguson (1972) as a dark northern form of this West Coast species.

Evolutionary Genetics in the 1930s

Sweadner wrote and published his hybrid zone paper during an auspicious time in the development of evolutionary theory, punctuated by the publication of key concepts in genetics and systematics. Unfortunately, he drafted his manuscript just before Dobzhansky's (1937) synthesis of these disciplines in the first edition of "Genetics and the Origin of Species." Darwin's concept of gradual evolution in response to natural selection had earlier fallen into a kind of disrepute (Edey and Johanson, 1989), due largely to the work begun by T. H. Morgan in about 1911 and continued by Hermann Muller from the 1920s into the 1950s, using mutations as chromosome markers in *Drosophila*. Such mutations produced sudden, discrete, and often dramatic phenotypic change, which these workers proposed as a more likely mechanism of evolutionary change.

During this period, Fisher (1930) and Haldane (1932) developed a mathematical theory of gene frequency change in interbreeding populations subject to the effects of natural selection. To this body of population genetics theory, Wright (1932) contributed the role of inbreeding and the effect of genetic drift in small populations. Systematists of the time, including Sweadner, were confounded by the contrast between the geographic variation they observed in nature—often subtle, gradual, and clinal—and the abrupt and dramatic variation seen in the *Drosophila* laboratories. The newly formulated mathematics of population genetics offered little practical insight into the mechanism of speciation and evolution, partly because these abstract concepts of genes and alleles were difficult to relate to the complex characters systematists studied in the field and using museum specimens. The chemical structure of DNA, the fundamentals of transcription and of protein synthesis, and other basic aspects of gene expression were yet to be discovered. While the new genetic concepts strengthened Darwinism by providing a genetic basis for the origin of adaptations, they did not deal with the areas of weakness in Darwinian theory: the genetic changes that occur during speciation, and the properties that allow species to maintain their integrity in sympatry.

Dobzhansky (1937) combined the important elements of population genetics, the genetic and phenotypic variation seen in the field, and the genetic differences between species (largely from laboratory breeding of *Drosophila*) into the first modern synthesis of evolutionary thought (Coyne, 1994). Dobzhansky (1937) described speciation in terms of the origin of reproductive isolation, but since this work appeared the same year as Sweadner's (1937) monograph on the *Platysamia*, Sweadner was denied this insight into the genetics of speciation. Ironically, subsequent editions of Dobzhansky's book cited Sweadner's paper as an example of introgressive hybridization, the first step in the origin of species before the appearance of effective reproductive isolation.

Sweadner's Work and Subsequent Studies of Hyalophora

Breeding studies dating back to the turn of the century (Morton, 1895; Soule, 1902) showed that the members of the genus *Hyalophora* (which includes the familiar cecropia moth) lack effective mating barriers, and interspecific hybrids could be produced easily in captivity. Reared female hybrids are typically barren, but F_1 male hybrids are usually fully fertile and can be backcrossed to either parent species. Sweadner (1934) conducted such studies using stock of *H. cecropia*, *H. columbia gloveri*, and *H. euryalus* and found that females of these species readily mated with males of any other species in captivity, and that tethered females would attract and mate with wild males of other species in a natural setting. Given the lack of mating barriers, it seemed likely that extensive hybridization would occur wherever the ranges of any two *Hyalophora* overlap. Even if hybrid females were barren, backcrossing by male hybrids might lead to intergradation between the forms in this region of initial hybridization.

A population of *Hyalophora* from the vicinity of Kaslo, British Columbia, had been described by Cockerell (1914) as *Samia rubra kasloensis*. Examination of specimens by Sweadner suggested to him that phenotypic variation in "*kasloensis*" might represent hybrid intergradation between the West Coast species *H. euryalus* (= *S. rubra*) and the Rocky Mountain species *H. gloveri*. Subsequent authors now consider the latter a subspecies of *Hyalophora columbia* (Collins, 1973; Kohalmi and Moens, 1975, 1988; Lemaire, 1978; Tuskes et al., 1996). In this paper I refer to populations of *Hyalophora* in the Bitterroot region simply by the name *kasloensis*, without quotes, as a convenience in communication and not in a formal taxonomic sense.

During a survey trip in 1932 to the Bitterroot Mountains of Idaho and Montana, Sweadner used a trap line of tied *Hyalophora* females to obtain samples along a transect from near Helena, Montana, west over Lookout Pass to Coeur d'Alene, Idaho. These locales appeared to represent the termini of a complete intergradation between the parent species. Using graphs and charts of wing character measurements, Sweadner (1937) represented this intergradation in what is one of the first uses of a hybrid index. Although Sweadner obtained 61 hybrid pairings, the difficulty of transcontinental travel prevented him from rearing larvae and conducting an extensive program of experimental hybridization. He was able to match laboratory *H. columbia gloveri* × *H. euryalus* hybrids with wild specimens to further substantiate his theory of the origin of *kasloensis* through natural hybridization, which he proposed occurred as the result of postglacial range extensions from Ice Age refugia.

Sweadner made a second survey to investigate the possibility of natural hybridization between *H. cecropia* and the subspecies of *H. columbia*. The small, dark form *H. c. columbia* and *H. cecropia* are sympatric in the region of the Great Lakes; *H. cecropia* also contacts the larger, brighter form *H. columbia gloveri* along the eastern escarpment of the northern Rocky Mountains and in the prairies of Manitoba. Neither Sweadner (1937) nor Collins (1973) discovered evidence of extensive intergradation.

In his concluding remarks, Sweadner (1937:221) included a synopsis of contemporary species concepts and presented surprisingly modern insights provided by *Hyalophora* concerning the process of speciation. He interpreted the lack of complete reproductive isolation among the *Hyalophora* as an example of the gradual nature of speciation and of discordance in rates of evolution of various characters. In discussing the limitations of morphological criteria, such as genitalia in Lepidoptera, he stated: "Another system is the conception of Rassenkreise or Formenkreise in which the various local races. . .are placed together in a sort of a super species. The basis of differentiation is the tendency to pair." Here he presages Dobzhansky's (1937) use of reproductive isolation as a species criterion, but then states: ". . .the genus [*Hyalophora*] would make an excellent Formenkreise, *but the female hybrids are all sterile*, and the continuance of the hybrid race [is] dependent on backcrossing to the parent species by the males." This problem of female barrenness, as seen in lab crosses, troubled Sweadner, who did not realize that females with normal fecundity can occur within hybrid zones.

By uniformly characterizing taxa, Sweadner was somewhat typological in his thinking, but at this time population genetics was not a part of traditional systematics and taxonomy. Nevertheless, he did recognize that different classes of traits may evolve at different rates: "Often two forms may be morphologically distinct but physiologically alike. . . . These forms or subspecies freely interbreed and produce fertile offspring. Usually physiological differentiation lags behind morphological differentiation." In his conclusion he remarks that "The genus *Platysamia* [= *Hyalophora*]. . .illustrate[s] the futility of attempting to set up rigid universal criteria for defining the limits of species."

Hybrid Zones in Studies of Speciation

The potential of hybrid zones to reveal evolutionary processes, only now being realized by evolutionary biologists, lured Sweadner into undertaking a challenging, even dangerous, cross-continental trek in the 1930s. Decades later, early students of hybrid zones (Sibley, 1954; Short, 1969) interpreted them as examples of the continuous and gradual nature of speciation. Under this interpretation, allopatric populations were assumed to have diverged in morphological and other characteristics, but to have lacked effective reproductive barriers; upon secondary contact the two taxa freely interbred, establishing a population of hybrids, identified by traditional morphological criteria. It was thought that hybrids were somehow unfit, due to low viability, sterility, or disruption of ecological adaptations, but few studies involved experimental breeding to test these ideas. Hybridization in nature between distinct taxa challenged the biological species concept based strictly on reproductive isolation. The disruption of "coadapted gene complexes" in hybrid genomes was thought to provide the basis in natural selection for the perfection of incipient reproductive isolation (Dobzhansky, 1951, 1971). On these grounds, hybrid zones were considered to be transitory phenomena.

Bigelow (1965) offered a descriptive model arguing against the origin of reproductive isolation in hybrid zones, thus partly explaining their stability. When hybrid unfitness is severe, the very condition thought to favor the origin of antihybridization mechanisms, Bigelow's (1965) model predicted that the barrier to introgression of foreign genes between species across the zone would be greater. Most matings just outside the zone will be between individuals with pure parental genotypes, and therefore these populations would not be subject to selection to prevent hybridization. Moreover, any change in mating behavior or physiology likely would be selected against in the parental populations as it would disrupt homospecific mating.

Slatkin (1973) and Endler (1977) discussed hybrid zones in terms of cline theory, in which they used computer models to examine the effect of varying rates of gene flow on gene frequencies for a single locus under selection by an environmental factor. In their models: (1) a gradient in selection intensity can produce a corresponding cline in the frequency of such genes, even in the face of gene flow; and (2) sharp clines form under conditions of strong selection and low dispersal, whereas gradual clines form where selection is weak and gene flow rates are higher. Under these conditions, reproductive isolation can evolve if linkage occurred between a gene under strong selection and a locus controlling critical mating traits, a process termed parapatric speciation. These theoretical studies served as an admonition to critically re-examine the common assumption in hybrid zone studies of secondary contact after divergence in allopatry.

By the early 1980s, enzyme electrophoresis and other techniques in molecular genetics, combined with multivariate morphometrics, had spawned a new generation of hybrid zone studies. This empirical research inspired population geneticists to formulate detailed computer models of hybrid zones. Such models typically used cline theory and diffusion equations to predict the effects of selection and dispersal on gene exchange and introgression (Moore, 1977; Barton and Hewitt, 1981, 1985, 1989). The narrow width of hybrid zones, bounded by sharp phenotypic boundaries, were thought to reflect an equilibrium between dispersal, tending to broaden the zone, and selection against unfit recombinant genotypes, tending to narrow the zone of intergradation.

Hybrid zones are now seen as productive natural laboratories in studies of speciation (Hewitt, 1988, 1989, 1993; Harrison, 1990, 1993; Collins, 1991). The genetic similarity of hybridizing taxa, and the degree of genetic introgression across hybrid zones, can be estimated directly from allozyme and sequencing data. When estimates of dispersal rates are available, the shapes of clines can reveal the relative strength of selection on given alleles. Data collected on reproductive isolation relate directly to the process of speciation. Prezygotic isolation can be observed in the field, and can be studied in the lab for those organisms amenable to experimental manipulation. An understanding of postzygotic isolation and overall developmental genetic compatibility must be derived from laboratory hybridization and the rearing of experimental broods. The historical factors surrounding the origin of hybrid zones are the most difficult to determine (Harrison, 1990).

Collins (1984) analyzed a population of hybrids between *H. euryalus* and *H. columbia gloveri* near Lake Tahoe in the California Sierra Nevada Mountains. This population exhibited a great deal of phenotypic variation, exceeding that seen in reared primary hybrids, suggesting extensive backcrossing and genetic recombination. Female intergrades were fully fecund, unlike barren hybrid females produced by crossing allopatric stocks of *H. euryalus* and *H. c. gloveri*. With this work as background, in this paper I re-examine Sweadner's (1937) proposed hybrid origin for these Bitterroot populations of *Hyalophora*. Laboratory F_1 hybrids of known parentage served as reference standards in comparison with wild-collected and reared stock in experimental hybridization and multivariate morphometric analyses. The results of experimental hybridization are considered with respect to the taxonomy of intergrade populations in the Northwest and an interpretation of the phylogeny and patterns of speciation in the genus. The origin of hybrid zones is discussed in terms of current concepts of Pleistocene and postglacial biogeography.

METHODS AND MATERIALS

Collecting and Rearing Livestock

Wild males for use in discriminant analysis and for breeding stock were collected using funnel traps baited with a virgin *Hyalophora* female confined in a small cage above the funnel opening. Males responding to the "calling" female persistently fluttered about the vicinity of the small cage, and upon touching the smooth metal funnel usually slid through its opening. This type of moth trap has proven very effective for many species of saturniids (Collins and Weast, 1961; Collins, 1974, 1984). While Sweadner was able to tie out only single females along a trap line, a series of such funnel traps can obtain large samples over a wide area in a few days. All western taxa and populations of *Hyalophora* emit pheromone from about 0300 hours until dawn (Sweadner, 1937; Collins, 1984). The genus is entirely univoltine and adults emerge in a concentrated flight period in late spring and early summer. Following a few preliminary field trips, I extensively trapped moths during late May and early June from 1989 through 1995 throughout Idaho and eastern Montana.

Females of native *Hyalophora* were collected at ultraviolet light traps, and occasionally at outdoor commercial lights. Such females usually have laid most of their ova, but often contain enough ova to start laboratory colonies. While no larvae or live cocoons of *kasloensis* were collected, immatures of *H. euryalus* and *H. c. gloveri* were collected in California, and reared stock of *H. c. gloveri* from Utah and of *H. c. columbia* from Ontario were obtained from local collectors.

Matings for specific experimental broods were obtained by confining males and females in nylon mesh cages or by enclosing a virgin female in the screen cage below the trap funnel, where she mated with a wild male after he entered the trap. Adult saturniids do not feed, and eclose with their entire complement of mature ova. Mated *Hyalophora* females readily oviposited in paper bags in the absence of a host plant. After oviposition was complete, usually after three to four days, ova were stored by cutting the paper bag into small pieces which were placed in plastic petri dishes, and stored at room temperature. The fecundity of a female was determined simply by counting the total number of ova laid; rarely, examination showed that a female still contained a significant number of ova, and these were dissected out and counted.

Unless otherwise noted, listed fecundity rates reflect the number of ova actually laid. After four or five days, infertile ova usually collapse, and infertility can be estimated reliably by counting these distorted ova. Most embryos that fail to hatch had attained nearly full development; the egg turns dark as normally occurs just prior to hatching, but the ovum does not collapse. An estimate of developmental genetic incompatibility is obtained easily by counting such unhatched ova, and in doubtful cases the ova can be dissected and examined under low magnification. Some errors occur where early embryo death is confused with infertility, but by these methods great numbers of ova (about 200 per female on average) were scored for female fecundity, percent fertile, and percent viable (hatched/fertile). Compatibility data were analyzed using pairwise Student's *t*-tests (BMDP-3D two-group test; Dixon, 1992) on arcsin-transformed percentages. Interpopulation crosses for *H. euryalus* and *H. c. gloveri* (Collins, 1984) were used for comparison. For analysis of fecundity, forewing length was chosen instead of weight to compensate for individual size variation because a large portion of the mass of a gravid female is ova whereas sterile hybrid females may be large but lack ova.

Larvae were reared by stapling a piece of paper containing typically 20 ova to a leaf of a host plant, and covering the branch with a strong, nylon mesh bag. Lots were divided up as larvae matured, and larvae were transferred to fresh foliage by cutting the twig or branch to which they were attached. Cocoons were collected after larvae spun in the bag. The great majority of larvae were reared on *Prunus emarginata* (bitter cherry) at about 1700 m in Nevada County, California. This host was accepted readily by all broods, produced large, healthy larvae, and is a known natural host for native *Hyalophora* throughout much of the western United States (Collins, 1984). Survival was typically 80% or more, although occasionally mice or vespid wasps were able to enter the sleeves. To assess the suitability of several other host plants, some broods were reared at lower elevation on various *Ceanothus* (Rhamnaceae) and other hosts, and others were sleeved on *Salix exigua* (coyote willow) along streams in Mono County, California. Cocoons were stored at 4°C in a refrigerator, and subsequently were incubated in screen cages in an outdoor insectary. By storing newly emerged, virgin females at high humidity in a refrigerator or ice chest, their normal life span of a week to ten days could be extended greatly, and a reliable supply of females could be taken into the field for use in traps and as mating stock. Collected males could be stored similarly for mating or until they could be spread. Accounts of life history and descriptions of immature stages are based on data acquired while collecting adults and rearing experimental broods.

Collecting localities for specimens used in discriminant analysis and for stock in experimental hybridization were as follows: **Montana**: Bearmouth, Granite County, 33 mi E Missoula, 3800 ft; Lolo Hot Springs, Missoula County, 7 mi E Lolo Pass, 4200 ft; 7 mi E Milltown, Missoula County, 3300 ft; Rock Creek, Missoula County, 22 mi E Missoula, 3750 ft; Sula, Spring Gulch campground, Ravalli County, 4420 ft. **Idaho**: Atlanta, Elmore County, 5600 ft; Gibbonsville, Lemhi County, 32 mi N Salmon, 4290 ft; Wild Goose campground, Idaho County, 20 mi E Kooskia, 1720 ft; intergrade population, NE of Boise: a transect from Idaho City–Mores Creek Summit–Clear Creek Canyon–Lowman (Helende and Bonneville campgrounds) to Banner Summit; Wallace to Kellogg, Shoshone County, 2700 ft. **California**: Banner Mountain, 5 mi E Nevada City, Nevada County, 3000 ft; Mulholland Canyon, Los Angeles County; Nevada County, 17 mi E Nevada City, 5000 ft Hwy 20; W of Donner Lake, Nevada County, 6200 ft; E slope Monitor Pass, Mono County, 6000–7250 ft; Panamint Mountains, Thorndike campground, Inyo County, 7500 ft; Big Pine Canyon, Inyo County, 7850 ft. **Nevada**: E Humboldt Range, Elko County. Oregon: 10 mi N Burns, Harney County, 4000 ft.

Discriminant Analysis

The principles and application of discriminant analysis in systematics are well known (Bookstein et al., 1985). Populations used as reference samples were selected based on their geographic proximity to suspected hybrid zones. Each reference sample was far enough removed from areas of intergradation to ensure that gene flow did not influence adult phenotypes. The *H. euryalus* reference sample was composed of specimens from northern California counties bordering Oregon. The reference sample for *H. columbia gloveri* included males from Boulder, Larimer, and Routt counties, Colorado. F_1 hybrids were made using *H. euryalus* females from Alpine County, California, and male *H. c. gloveri* from western Nevada. In addition to the reference samples and wild-collected adults, I was able to borrow the entire *Hyalophora* collection amassed by W. R. Sweadner, including wild material and reared specimens, from the Carnegie Museum of Natural History.

Wing characters and methods of measurement and scoring were modified from Collins (1984). Initially, a suite of 24 characters was submitted for stepwise discriminant analysis (program 7M, BMDP Statistical Software, Inc.; Dixon and Brown, 1990). These characters included both quantitative characters (e.g., wing length and eyespot length) and numerically scored qualitative characters (e.g., color of postmedial band). Initial analysis showed that six characters produced a discriminant function that correctly identified the three reference groups: ratio of length/width hindwing discal spot (F = 189.30, df = 2, 106); color forewing postmedial band (F = 93.62, df = 4, 210); presence/absence hindwing discal spot touching postmedial line (F = 83.85, df = 6, 208); shape of forewing basal band (F = 74.05, df = 8, 206); color ventral forewing band (F = 64.73, df = 10, 204); forewing length (F = 58.41, df = 12, 202).

Each individual was assigned to one of the reference groups: *H. euryalus*, *H. c. gloveri*, or their F_1 hybrid. By analyzing the frequency distribution of distance values for each reference group, I determined criteria to assign an individual specimen to one of five classes, where classes 2 and 4 represent an intermediate position between *H. euryalus* and the F_1 hybrids, or between *H. c. gloveri* and the hybrids, respectively. Experience from the Sierra Nevada study had shown that many hybrid zone specimens fell into these classes, roughly corresponding to backcross individuals.

I had intended to rescore Sweadner's intergrade specimens and compare my discriminant classifications to his phenotype scores. Unfortunately, while Sweadner's original data labels and code numbers remain affixed to most specimens, no field or lab notebooks were found containing the character scores for any of his specimens, precluding these comparisons.

RESULTS

Genetic Compatibility

Hatch rate for interpopulation matings among *kasloensis* broods ranked lower than those for pure *H. euryalus* or *H. c. gloveri*, reciprocal F_1 crosses with these species, or even those for *kasloensis* × *H. c. columbia* or *H. euryalus* × *kasloensis* matings; this ranking was obtained also for "non-sib" *kasloensis* matings (Table 1). Of the 15 groups, the eight crosses with lowest index (percent hatched per ova laid) values involved *kasloensis* (Table 2). Data supplied by Dean Morewood (personal communication) also showed a degree of incompatibility between *H. euryalus* from the vicinity of Victoria, British Columbia, and *kasloensis* from the Okanagan Valley, interior British Columbia (Table 1).

Fertility in interpopulation crosses within *H. euryalus* is significantly higher than in test crosses within *H. c. gloveri*, although the source populations of *H. c. gloveri* were as widely separated as Utah and California (Table 3). All crosses of *H. euryalus* were from within California, except for two crosses with stock from Victoria, British Columbia (× male, Nevada County, California = 96.9%; × female, Los Angeles County, California = 81.1%). Viability rates were not significantly different for *H. c. gloveri* vs. *H. euryalus* (Table 4).

Using interpopulation matings for *H. c. gloveri* as a conservative standard, the fertility rate for pooled *kasloensis* ranked significantly lower, but non-sib matings for *kasloensis* did not differ significantly (P = 0.29; Table 3). Pooled reciprocal F_1 crosses between *H. euryalus* and *H. c. gloveri* also had significantly higher

Table 1.—*Compatibility indices in experimental crosses (female × male) between* Hyalophora "kasloensis" *and congeners: fecundity (number of ova laid), fertility (percentage of ova laid that were fertile), and viability (percentage of fertile ova that hatched),* (N) *= number crosses for pooled data.*

Group, cross	Fecundity	Fertility	Viability
I. Intrapopulation *H. kasloensis*			
1. female to UV Lolo Hot Springs, Montana	57	94.7	98.2
2. progeny above × sib	117	100.0	85.8
3. progeny 1 × Milltown, Montana	107	80.8	81.0
4. progeny II-6 × Sula, Montana	142	66.7	100.0
5. progeny II-6 × sib	168	64.6	67.7
6. progeny 5 × progeny 4	155	40.2	81.4
7. progeny 5 × sib	168	80.4	61.1
		75.3	82.2
II. Interpopulation *H. kasloensis*			
1. Lolo Hot Springs × Sula	106	66.7	79.5
2. Lolo Hot Springs × Wild Goose Campground, Idaho County, Idaho[1]	158	93.8	100.0
3. progeny 1 × Sula	140	90.8	92.8
4. progeny 1 × progeny I-3	181	99.4	95.6
5. progeny 1 × sib	168	81.0	95.0
6. progeny II-4 × progeny 3	133	80.4	91.0
7. progeny 6 × Wallace, Idaho	177	99.2	96.7
8. as above	125	84.4	98.7
		87.0	93.7
Pooled *H. kasloensis* nonsib matings (10)		85.7	93.4
Pooled *H. kasloensis* sib matings (5)		73.2	78.2
Data from D. Morewood (personal communication):			
1. Okanagan Valley, British Columbia, Canada × same	239	95.4 hatched/laid	
III. *H. euryalus* × *H. kasloensis*			
1. Banner Mountain, Nevada County, California × Lolo Hot Springs	180	92.8	100.0
2. Donner Lake, Nevada County, California × west Lolo Hot Springs	171	76.7	95.3
3. Banner Mountain × Bearmouth, Montana	164	92.1	99.3
4. Banner Mountain × Milltown, Montana	148	93.2	99.3
5. as above	102	0[2]	0
		88.7	98.5
IV. *H. kasloensis* × *H. euryalus*			
1. progeny II-2 × Banner Mountain (female small)	92	80.4	0
2. progeny II-2 × Nevada County, California (female small)	30	96.7	100.0
3. progeny I-1 × Nevada County	130	98.4	100.0
4. progeny II-1 × Banner Mountain	170	99.4	100.0
5. progeny I-2 × Banner Mountain	188	85.0	96.9
6. progeny I-3 × Banner Mountain	171	90.1	98.7
7. progeny II-5 × Burns, Oregon	122	82.0	99.0
		90.3	84.9
Data provided by D. Morewood (personal communication):			
1. Okanagan Falls, British Columbia, Canada × Victoria, British Columbia, Canada	69	69.6 hatched/laid	
2. as above	95	80.0 hatched/laid	
3. as above	106	90.6 hatched/laid	

Table 1.—*Continued.*

Group, cross	Fecundity	Fertility	Viability
V. F_1 hybrid (*H. euryalus* × *H. kasloensis*)			
1. (progeny III-3) × Gibbonsville, Idaho *gloveri*	164	77.5	96.8
2. as above	176	79.2	100.0
		78.4	98.4
3. as above × Nevada County *euryalus*	54	87.0	74.5
4. (Banner × Bearmouth) × Banner Mountain *euryalus* (retained 65 ova; 97 total)	32	88.9	68.8
5. (Banner × Milltown) × Nevada County *euryalus*	131	71.4	97.8
		82.4	80.4
6. (Banner × Milltown) × progeny II-3 *kasloensis*	108	93.5	91.1
		82.9	88.2
VI. F_1 hybrid (*H. kasloensis* × *H. euryalus*)			
1. progeny IV-2 × Banner Mountain *euryalus*	62	93.4	100.0
2. as above	59	96.6	98.3
		95.0	99.2
3. progeny IV-3 × *kasloensis* progeny II-5	130	37.1	87.0
VII. *H. c. gloveri* × *H. kasloensis*			
1. California: [(Monitor Pass-Big Pine) × Big Pine] × Wild Goose	123	65.9	50.6
2. as above × 3 mi east Lolo Hot Springs	184	47.8	48.9
3. (Monitor Pass) × Rock Creek, Montana	176	77.3	78.7
4. (Walker River × Monitor Pass) × 3 mi east Milltown	175	0[2]	0
5. Walker River × progeny II-1	276	99.0	100.0
6. Walker River × progeny I-4	184	92.4	97.1
		76.5	75.1
VIII. *H. kasloensis* × *H. c. gloveri*			
1. progeny II-1 × Gibbonsville	193	98.5	98.5
2. Lolo Hot Springs × Walker River	145	84.0	93.0
3. Lolo Hot Springs × Gibbonsville	163	69.3	94.9
4. as above	144	74.7	95.8
5. progeny II-6 × east Humboldt Range, Elko County, Nevada	173	74.2	97.8
		80.1	96.0
IX. F_1 hybrid (*H. c. gloveri* × *H. kasloensis*)			
1. F_1 (Monitor Pass × Rock Creek) × Lolo Pass *kasloensis*	94	89.6	98.8
2. *kasloensis* progeny II-5 × F_1 progeny VII-5	69	37.1	87.0
3. as above	196	56.0	71.9
4. II-5 *kasloensis* × (*gloveri* × *kasloensis*) VII-5	69	37.1	76.9
5. as above	196	56.0	71.9
X. F_1 hybrid (*H. kasloensis* × *H. c. gloveri*)			
1. F_1 progeny VIII-1 × F_1 progeny VIII-2	65	4.6	33.3
2. F_1 progeny VIII-1 × progeny II-3 *kasloensis*	0		
3. as above	2	0	0
4. progeny VIII-3 × progeny II-4 *kasloensis*	1	0	0
5. progeny VIII-1 × Boise County, Idaho hybrid zone	40	10.0	100.0
XI. *H. c. columbia* × *H. kasloensis*			
1. *columbia* Ontario, Canada × Sula	134	75.5	98.2
2. (*c. columbia* Ontario, Canada × *gloveri* Panamint Mts., California) × Milltown, Montana	236	88.5	97.9

Table 1.—*Continued.*

Group, cross	Fecundity	Fertility	Viability
3. *c. columbia* Ontario, Canada × progeny II-1	126	49.2	62.9
		71.7	86.3
XII. *H. kasloensis* × *H. c. columbia*			
1. Lolo Hot Springs × *columbia* Ontario, Canada	127	95.2	96.0
XIII. F_1 hybrid (*H. c. columbia* × *H. kasloensis*)			
1. progeny XI-3 × progeny II-4 *kasloensis*	143	92.3	72.0
2. as above	37	66.7	43.8
3. progeny XI-1 × *kasloensis* Sula	117	34.4	45.2
4. progeny I-2 *kasloensis* × progeny XI-1 F_1: infertile mating, ♀ retained ova			
5. progeny XI-1 × *c. columbia*	0		
6. progeny XI-1 × *gloveri* east Humboldt Range, Nevada	121	77.4	100.0
7. progeny 6 × *gloveri* Denver, Colorado	99	46.5	87.0
8. (F_1 *kasloensis* × *c. columbia*) × *c. columbia*	barren		
9. (as above) × *gloveri*	barren		
XIV. *H. kasloensis* × Boise County, Idaho, intergrade population			
1. progeny II-1 × Helende Campground	109	95.4	95.2
2. progeny II-6 × 9 mi east Idaho City	210	92.6	94.0
3. progeny II-5 × Lowman	131	18.4	100.0
		68.8	96.4
XV. *H. euryalus* × Boise County, Idaho, intergrade population			
1. Mulholland × Helende	175	100.0	100.0
2. Mulholland × Bonneville Campground	127	97.6	100.0
3. Banner Mountain × 10 mi north Idaho City	145	89.7	99.2
4. as above	187	92.8	100.0
		95.0	99.8
XVI. F_1 (*H. euryalus* × *H. kasloensis*) × Boise County, Idaho, intergrade population			
1. (Banner Mountain × Milltown) × Lowman	121	80.0	92.7
2. progeny above × Clear Creek Canyon	206	100.0	99.5
3. as above	162	97.2	98.6
4. progeny 2 (old female) × Clear Creek Canyon	157	40.1	98.4
5. progeny 2 (old) × Boise River *gloveri*	169	61.6	99.0
6. progeny 5 × (3) Idaho City	151	58.3	98.4
XVII. *H. c. gloveri* × Boise County, Idaho, intergrade population			
1. (Walker River × sib) × Atlanta, Idaho	277	91.9	80.1
2. (Utah × sib) × Clear Creek Canyon	214	98.1	100.0
3. (Utah × sib) × Clear Creek Canyon	200	98.1	99.4
		96.0	93.2
XVIII. Reference crosses, pooled data[3]			
1. interpopulation *H. euryalus* (15)	213.5	97.0	98.7
2. interpopulation *H. c. gloveri* (8)	215.3	91.5	99.5
3. *H. c. gloveri* × *H. euryalus* (8)	255.7	91.7	98.0
4. *H. euryalus* × *H. c. gloveri* (9)	197.1	91.2	96.9
5. *H. c. columbia* × *H. euryalus* (3)	131.7	71.9	93.1

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[1] Due to holdover pupae in diapause, sibs of parental broods in some cases were mated to progeny of these parental broods.

[2] Note: "0" values for fertility not entered in calculation of mean values.

[3] From Collins, 1984.

Table 2.—*Summary of genetic compatibility for* Hyalophora (n, *number of matings), arranged by decreasing index values: fertility (percent fertile of ova laid), viability (percent of fertile ova that hatched), and index (percent of ova laid that hatched).*

Origin, female × male (*n*)	Fertility	Viability	Index
Interpopulation *H. euryalus* (15)	97.0	98.7	95.7
H. euryalus × Boise, Idaho, Hybrid Zone (4)	95.0	99.8	94.8
H. kasloensis × *H. c. columbia* (1)	95.2	96.0	91.4
Interpopulation *H. c. gloveri* (8)	90.7	99.5	90.3
H. c. gloveri × *euryalus* (8)	91.7	98.0	89.9
H. c. gloveri × Boise, Idaho, Hybrid Zone (3)	96.0	93.3	89.5
H. euryalus × *H. c. gloveri* (9)	91.2	96.9	88.4
H. euryalus × *H. kasloensis* (4)	88.7	98.5	87.4
Interpopulation *H. kasloensis* (8)	87.0	93.7	81.5
H. kasloensis non-sib pooled (10)	85.7	93.4	80.0
H. kasloensis × *H. c. gloveri* (5)	80.1	96.0	76.9
H. kasloensis × *H. euryalus* (7)	90.3	84.9	76.7
H. kasloensis × Boise, Idaho, Hybrid Zone (3)	68.8	96.4	66.3
H. c. columbia × *H. kasloensis* (3)	71.7	86.3	61.9
H. c. gloveri × *H. kasloensis* (5)	76.5	75.1	57.5

fertility rates than those for pooled *kasloensis*, but did not differ from those for non-sib *kasloensis* ($P = 0.21$).

Again using *H. c. gloveri* as a standard, variation in viability among all groups was not significant except for both pooled and non-sib *kasloensis* (Table 4). Using *H. euryalus* as a standard, significant differences were found for all crosses involving *kasloensis*, including those involving female *kasloensis* × male *H. euryalus*.

In comparisons of hatch rate, female *H. euryalus* were the most compatible in crosses with other taxa, although the number of replicates involving female *H. c. columbia* is low (Table 2). Both reciprocal crosses between *H. c. gloveri* and *H. euryalus* showed a higher hatch rate than the crosses involving *H. c. gloveri* with *kasloensis*.

Wild males from the hybrid zone near Boise, Idaho, were more compatible with females of pure *H. euryalus* and *H. c. gloveri* than either of these species were when crossed with male *kasloensis*. Also, two of the three crosses (Table 1:group XIV) between a female *kasloensis* and a male from the Boise hybrid zone resulted in an average hatch rate of 88.9% (not shown in Table 1), only slightly lower than that for crosses with female *H. c. gloveri*. The high genetic compatibility between males from this zone and females of other taxa contrasts with that of the *kasloensis* populations. This trend may result from more balanced gene introgression in the Boise hybrid zone, in contrast with the asymmetrical *kasloensis* zone (see below). Crosses between female *kasloensis* and male *H. c. gloveri* from the Gibbonsville location showed reduced fertility rates, as did other crosses with more distant populations of *H. c. gloveri*.

Natural populations, ranked in order of decreasing absolute fecundity and fecundity indices, are: *H. cecropia*, *H. c. gloveri*, *H. euryalus*, and *kasloensis* (Table 5). The fecundity for female *kasloensis* is low, even given their smaller average wing size. The fecundity of female *H. euryalus* × *kasloensis* hybrids is substantially lower than that of *kasloensis* but greater than those of other hybrid combinations. While the fecundity of *H. c. columbia* × *kasloensis* females is much lower than that for "pure" taxon broods, the fecundity of these hybrid females

Table 3.—*Pairwise Student's* t-*tests (df) of arcsin-transformed fertility data for experimental broods of* Hyalophora: *statistic, probability. Reciprocal crosses pooled in some cases to increase sample sizes.*

Group (n)	*euryalus*	*eury.* × *glov.* *glov.* × *eury.*	*kasloensis* pooled	Non-sib *kasloensis* (11)	*kaslo.* × *eury.* (7)	*glov.* × *kaslo.* *kaslo.* × *glov.* (10)
H. c. gloveri[1] (8)	−2.74 (21)	−0.13 (23)	1.57 (19)	1.05 (17)	0.15 (13)	1.97 (16)
	0.012**[2]	0.899	0.133	0.308	0.884	0.067*
H. euryalus[1] (15)		2.689 (30)	4.11 (26)	3.76 (24)	2.57 (20)	4.62 (23)
		0.012**	0.0003***	0.001***	0.018**	0.0001***
H. euryalus × *H. c. gloveri*[1] (17)			2.07 (28)	1.31 (26)	−0.26 (22)	2.43 (25)
H. c. gloveri × *H. euryalus*			0.047**	0.202	0.796	0.22**
H. kasloensis (13) pooled				−0.49 (22)	1.32 (18)	1.07 (21)
				0.0629	0.203	0.297

[1] Collins, 1984; unpubl.

[2] NS ($P > 0.10$), * ($0.05 < P < 0.10$), ** ($0.01 < P < 0.05$), *** ($P < 0.01$).

Table 4.—*Pairwise Student's* t-*tests (df) of arcsin-transformed viability data for experimental broods of* Hyalophora: *statistic, probability. Reciprocal crosses pooled in some cases to increase sample sizes.*

Group (n)	*euryalus*	*eury.* × *glov.* *glov.* × *eury.*	*kasloensis* pooled	Non-sib *kasloensis*	*kaslo.* × *eury.* (7)	*glov.* × *kaslo.* *kaslo.* × *glov.* (10)
H. c. gloveri[1] (8)	0.51 (21) 0.614	1.51 (23) 0.145	3.59 (19) 0.002***[2]	2.93 (17) 0.009***	1.16 (13) 0.268	2.75 (16) 0.014**
H. euryalus[1] (15)		1.17 (30) 0.252	4.15 (26) 0.0003***	2.97 (24) 0.007***	1.43 (20) 0.167	3.26 (23) 0.003***
H. euryalus × *H. c. gloveri*[1] (17) *H. c. gloveri* × *H. euryalus*			3.47 (28) 0.002***	2.05 (26) 0.051*	−1.18 (22) 0.249	2.75 (25) 0.011**
H. kasloensis (13) pooled					−0.03 (20) 0.947[3]	1.06 (19) 0.304

[1] Collins, 1984; unpubl.

[2] NS ($P > 0.10$), * ($0.05 < P < 0.10$), ** ($0.01 < P < 0.05$), *** ($P < 0.01$).

[3] Probability shown is interpopulation *kasloensis*; intrapopulation = 0.166.

Table 5.—*Fecundity (number ova laid, mean ± SD), mean length of forewing, and their ratio among* Hyalophora *species and their hybrids.*

Group (n)	Fecundity	Forewing length	Fecundity/ forewing length
H. cecropia[1]	271.5 ± 69.5	75.0	3.62
H. euryalus (12)	175.5 ± 36.8	58.3 ± 4.6	2.99 ± 0.48
H. c. columbia (1)	134.0	55.0	2.44
H. c. gloveri (13)	221.1 ± 45.2	62.9 ± 4.2	3.52 ± 0.74
H. c. columbia × *H. c. gloveri* (4)	177.8	59.3	3.02
H. kasloensis (25)	149.6 ± 32.1	55.8 ± 2.3	2.62 ± 0.50
F_1 *H. euryalus* × *H. kasloensis* (6)	132.8	56.8	2.32
F_1 *H. c. columbia* × *H. kasloensis* (4)	79.5	55.8	2.07
F_1 *H. kasloensis* × *H. c. gloveri* (5)	21.6	57.9	0.36
Monitor Pass, Mono County, California hybrid zone (bred intergrades) (5)	222.0	64.2	3.46

[1] Index calculated from separate averages for fecundity (n = 32) and forewing length (15).

exceeded that of hybrid females from *kasloensis* × *H. c. gloveri* crosses; this pattern parallels that for hatch rate (Table 1). The fecundity of intergrade females from the Monitor Pass hybrid zone was comparable to that of pure *H. c. gloveri*. No data are available for females from the Boise hybrid zone. However, progeny from matings of wild Boise hybrid zone males with female (*H. euryalus* female × *kasloensis* male) hybrids were successively crossed for three generations to wild males in the Boise hybrid population, and consistently yielded females with a high fecundity (Table 1:group XVI, cross 1). This result suggests that the Boise hybrid population contains fully fecund females, similar to females from both *kasloensis* and the Monitor Pass hybrid population.

Pure *kasloensis* crosses yielded a normal ratio of males to females (Table 6), as did experimental, reciprocal crosses between *H. euryalus* and *H. c. gloveri* (Collins, 1984). Distortion of the sex ratio occurred in crosses between female *kasloensis* and male *H. euryalus*, and also in crosses between female *H. c. gloveri* and male *kasloensis*. Although the female offspring from matings between female *H. euryalus* and male *kasloensis* had only slightly lowered fecundities (Table 5), the sex ratio was distorted in the backcross brood involving these F_1 females and a pure *H. euryalus* male (Table 6). In general, sex ratios indicate an incompatibility in at least some combinations involving *kasloensis* and either *H. euryalus* or *H. c. gloveri*. The sex ratio of progeny from crosses of female *H. c. columbia*

Table 6.—*Deviation from 1:1 sex ratios in experimental hybrid broods for* Hyalophora.

Cross (female × male)	Number eclosed: Female	Number eclosed: Male	Chi-square value[1]
H. kasloensis	44	40	0.190^{NS}
H. euryalus × *H. kasloensis*	17	20	0.243^{NS}
H. kasloensis × *H. euryalus*	19	32	3.314*
H. c. gloveri × *H. kasloensis*	8	13	1.191^{NS}
H. kasloensis × *H. c. gloveri*	16	15	0.032^{NS}
H. c. columbia × *H. kasloensis*	13	11	0.167^{NS}
H. kasloensis × *H. c. columbia*	1	3	NSD
F_1 (*H. euryalus* × *H. kasloensis*) × *H. euryalus*	6	15	3.857**

[1] P-value: NS ($P > 0.10$), * ($0.01 < P < 0.05$), ** ($P < 0.01$); NSD = not sufficient data.

Table 7.—*Compatibility indices in experimental crosses (female × male) between* Hyalophora cecropia *and congeners: fecundity (number of ova laid), fertility (percentage of ova laid that were fertile), viability (percentage of fertile ova that hatched), hatch rate (percentage of ova laid that hatched).*

Group Locality	Fecundity	Fertility	Viability	Hatch rate
Intrapopulation *H. cecropia*				
Urbana, Illinois,[1] wild (11)	368.7			91.3
Urbana, Illinois, reared nonsib[1] (4)	277.0			96.2
Urbana, Illinois, wild	326	99.1	61.3	60.7
Denver, Colorado, wild	284	98.9	94.7	93.7
St. Louis, Missouri (avg. 35 pairings)[2]		85.5		77.0
Interpopulation *H. cecropia*				
Ohio, Hancock County × Iowa, Polk County	382	99.2	100.0	99.2
H. cecropia × *H. columbia gloveri*				
Madison, Wisconsin × Gallatin County, Montana	337	53.3	96.7	51.5
Urbana, Illinois × Salt Lake City, Utah[3]	204			0
As above	355			89.3
As above	425			87.1
H. columbia gloveri × *H. cecropia*				
Salt Lake City, Utah × Urbana, Illinois[3]	306			92.8
As above	190			85.8
As above	90			0
As above	228			90.8
As above five females: no ova laid				
H. cecropia × *H. c. columbia* (see text)				
H. cecropia × *H. euryalus*				
Illinois × Monterey, California[3]	292			55.1
As above	250			3.6
As above	265			1.1
Illinois × Nevada County, California	259	100.0	99.6	99.6
Three matings as above, normal number ova laid, all infertile				
H. euryalus × *H. cecropia*[4]				
Monterey, California × Urbana, Illinois[3]	200			71.0

[1] Waldbauer and Sternburg, 1979.

[2] Rau and Rau, 1913. Pedigree of stock not given, ova handled excessively.

[3] Unpublished data supplied by J. Bruce Duncan. All other data from author's unpublished research.

[4] This cross typically results in damage to the genitalia of the female *H. euryalus* by the claspers of the larger *H. cecropia* male (see text), preventing oviposition.

with male *kasloensis* was normal; too few progeny of the reciprocal cross were reared to test.

Available data indicate that the compatibility of *H. cecropia* with congeners is less than that between *H. euryalus* and *H. columbia gloveri* (Table 7). Fertility and viability are both normal in reciprocal crosses between the latter species (Table 1). Mechanical prezygotic isolation based on size difference and postzygotic genetic incompatibility is expressed in crosses between both *H. cecropia* and *H. c. columbia*, as well as in crosses between *H. cecropia* and *H. euryalus*. Tuttle (1985) found that captive *H. cecropia* typically resisted mating attempts of wild *H. c. columbia* males, or if cross-mated would re-mate conspecifically; oviposition rate and hatch rate were low in the few successful hybrid crosses. The large claspers of male *H. cecropia* physically damaged the genitalia of the smaller

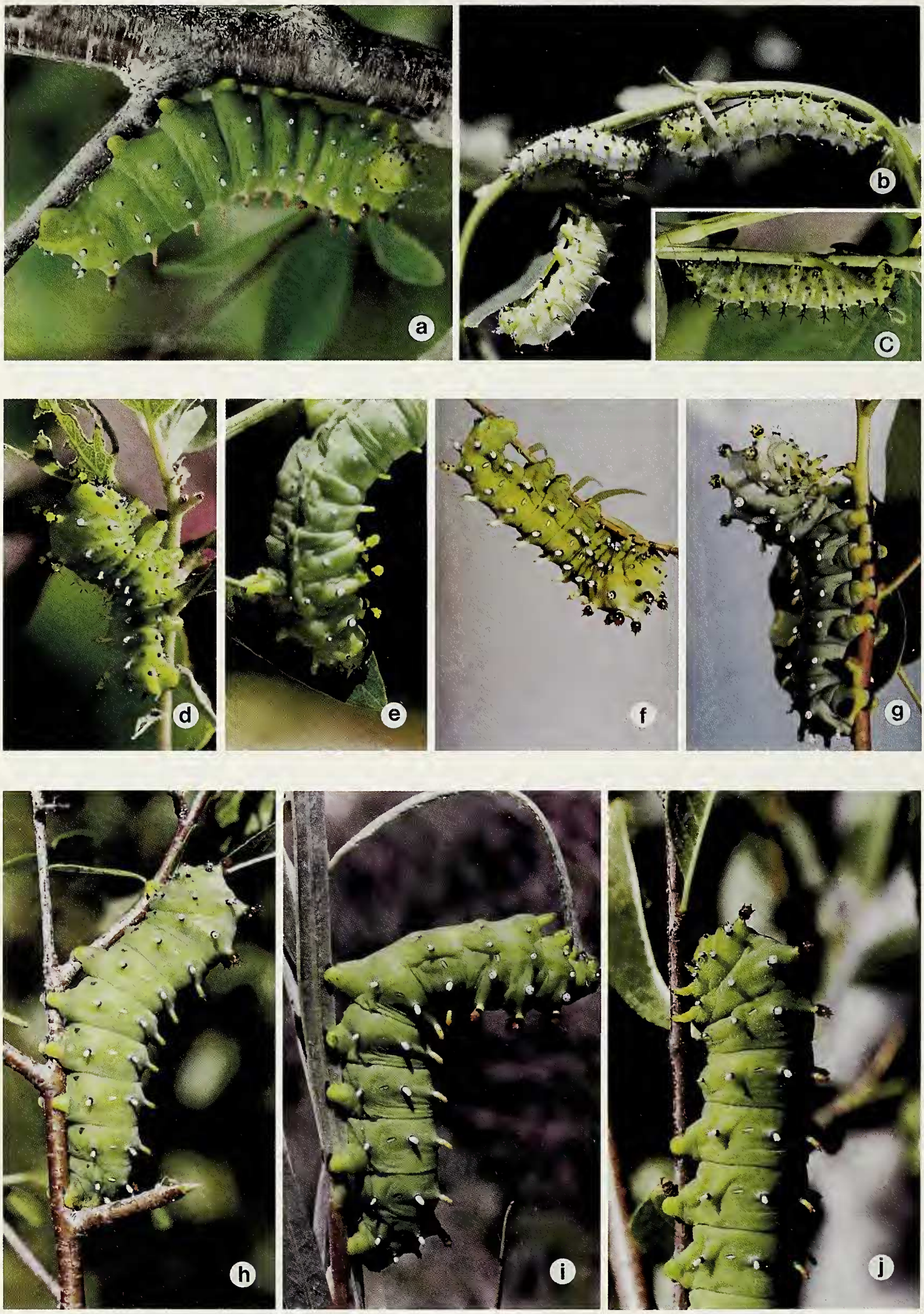

Fig. 1.—Larvae of *Hyalophora*. a–c, *H.* "*kasloensis*," Lolo Hot Springs, Missoula County, Montana. a, fifth instar, × .75; b, fourth instars, note variation in melanization of scoli, approx. × 1.0; c, third

H. c. columbia female in other hybrid pairings, preventing oviposition. The hatch rate of crosses between female *H. cecropia* and male *H. euryalus* is low (Table 7), and the reciprocal cross usually resulted in damage to the genitalia of *H. euryalus* (Weast, 1959; Collins and Weast, 1961; Tuskes et al., 1996). More infertile matings appear to occur in crosses between *H. cecropia* and *H. euryalus* than between the former and *H. c. gloveri.*

Available data suggest that *H. cecropia* is somewhat more compatible with *H. c. gloveri* than with either *H. c. columbia* or *H. euryalus*. Females of *H. c. gloveri* are only slightly smaller on average than *H. cecropia*, and mechanical prezygotic isolation apparently does not occur. Yet very few natural hybrids have been collected where these two species are sympatric on the east slopes of the northern Rockies and in the Canadian Prairie Provinces (Tuskes et al., 1996). Reproductive isolation in the wild has not been studied to date.

Life History and Immature Stages of Hybrid Populations

No complete description of the immature stages of *kasloensis* has been published. Sweadner (1937) was unable to obtain live material of *kasloensis* and the immature stages were unknown to him. He noted that the final instar of various hybrid larvae with a male *kasloensis* as a parent differed from all other *Hyalophora* taxa in that all the dorsal scoli were reddish. All other forms have yellow dorsal abdominal scoli in the final instar (Tuskes et al., 1996). Morewood (1991) confirmed the presence of red scoli in a brief description of British Columbia stock of *kasloensis*, and he illustrated the last two instars. The larval phenotypes from the Bitterroot Mountains appear similar to his descriptions (Fig. 1). The following descriptions (measurements in mm) are based on stock obtained from wild females collected near Lolo Hot Springs and Sula, Montana, and from broods resulting from mating these progeny to wild males (Table 1).

Ova.—Oval, not noticeably tapered; slightly dished on one side in viable ovum. Length: $\bar{x} = 2.34$, range 2.10–2.55. Width: $\bar{x} = 1.68$, range 1.63–1.74. Attached to surfaces by a dark reddish-brown gum-like cement. Ova of *H. euryalus* slightly larger: 2.56 × 2.08 average.

First Instar.—Length 8–10 at rest at end of stadium. Head, legs, prolegs, and scoli deep, shiny black. Integument dull black, developing dull yellow around base of spiny scoli as larva grows. The first instar larvae of *H. c. gloveri*, *H. euryalus*, and *kasloensis* cannot be separated reliably by any combination of characters.

Second Instar.—Length 12–15. Head black, sometimes with yellow-green medially. All scoli shiny black. Body at first dull yellow, changing to yellow-green with areas of yellow surrounding base of scoli by mid-instar. Black, diamond-shaped or wedge-shaped marks medially between dorsal scoli of all segments. Intersegmental black markings expressed to varying degrees. The second instar

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←

instar, × 1.25. d, e, *H. euryalus*, Nevada County, California. d, fourth instar photographed in nature, × 1.0; e, fifth instar, × .85. f, *H. c. columbia* fifth instar, Michigan, Livingston County, × 1.0. g, *H. columbia gloveri*, fifth instar, Utah, vicinity Salt Lake City, × 1. h, *H. "kasloensis"* ♀ × *H. c. columbia* ♂, fifth instar, × .75. i, *H. euryalus* ♀ × *H. "kasloensis"* ♂, fifth instar, × .80. j, *H. "kasloensis"* ♀ × *H. c. gloveri* ♂, fifth instar, × 1.0.

is also nearly identical to *H. c. gloveri*; most second instars of *H. euryalus* are somewhat brighter yellow, especially early in the stadium.

Third Instar.—Length 18–20. Head dull green with paired black marks tapering toward mouth. Body dull grey-green shading into yellow-green laterally, marked with small black dots ventrally. Prolegs and scoli black. The overall appearance is closer to *H. c. columbia*, which has black scoli in the third instar, than to *H. c. gloveri*, which may have orange dorsal scoli and blue lateral scoli, often black at tips. In this instar *H. euryalus* has bright yellow dorsal and light blue lateral scoli, with no tendency toward melanization. Some *H. euryalus* populations in extreme southern California and Baja California may have orange dorsal scoli.

Fourth Instar.—Length 33–38. Head and integument dull blue-green, shading to faint yellow tinge laterally and on prolegs. Dorsal thoracic and dorsal first abdominal scoli a deep coral red, encircled with black at base. In about one-half of larvae examined the dorsal abdominal scoli are red-orange to light orange, with light blue lateral scoli. Other larvae have all scoli black at tip, showing color only at base. Approximately one-fourth of larvae have all black lateral and dorsal scoli on all segments. Setae black in all color forms. This range of scoli color variation may be seen in one brood. A similar variation is seen in *H. c. gloveri*, which would be difficult to separate from *kasloensis*, except for a tendency to have somewhat stouter scoli with more prominent setae. Fourth instar *H. c. columbia* invariably has all scoli a deep, shiny black, and this phenotype is also identical to the corresponding variation in *kasloensis*. The fourth instar of *H. euryalus* has yellow dorsal scoli, and light blue lateral scoli, and never expresses the melanic variation seen in the subspecies of *columbia* or in *kasloensis*.

Fifth Instar.—Length 65–80. Head and integument dull green to dull blue-green, similar to *H. c. gloveri*. Dorsal thoracic scoli and dorsal scoli on first abdominal segment deep coral red. These three pairs of scoli encircled at base with a series of irregular black markings. Remaining dorsal abdominal scoli red to red-orange. Lateral scoli on all segments light blue, blue-white at tip, black at base. Both *H. c. gloveri* and *H. euryalus* have all dorsal scoli yellow. The enlarged dorsal thoracic scoli and dorsal first abdominal scoli in *H. euryalus* are encircled with a prominent black band of even width. This marking in *H. c. gloveri* and *H. c. columbia* is irregular, often in the form of blotches, just touching. The corresponding black marking in *kasloensis* is intermediate. The dorsal thoracic and first abdominal scoli in *H. c. columbia* are the same deep red as in *kasloensis*, the remaining dorsal abdominal scoli are yellow to pinkish-yellow. In *H. euryalus*, all scoli other than the dorsal thoracic are often more elongated than in other taxa, which have scoli of a more spherical or bulbous shape. In this regard, *kasloensis* resembles more closely the subspecies of *H. columbia*.

Cocoon.—All *Hyalophora* spin a double-walled cocoon with a loose intervening mesh. At one end is an eclosion valve, made up of strands spun parallel and tapering to a point. The cocoon of *H. c. gloveri* is compact and adorned with silvery or golden bands of silk. The cocoon is impregnated with a fluid which darkens the silk, except for the distinctive bands. These cocoons are dull brown to grey, and in color and texture resemble bark and dried leaves. The larvae of *H. c. gloveri* usually spin at the base of the host or in nearby dense vegetation. The northern subspecies *H. c. columbia* spins a smaller, darker, and often more compact cocoon, which is very cryptic against the bark of its host, tamarack (*Larix laricina*). The cocoon of *H. euryalus* tends to be ovoid to almost round, except for the valve end, somewhat resembling a Florence flask. The *H. euryalus* cocoon is usually grey, and may be shiny in texture, but lacks the striations of *H. c. gloveri*. The larvae of *H. euryalus* usually spin the cocoon among the branches of the host plant. The cocoon of *kasloensis* is intermediate between *H. c. gloveri* and *H. euryalus* in shape and texture, possessing the banding of *H. c. gloveri*, but usually not as compact. I have collected only two cocoons of *kasloensis* in the wild; both were spun among dense vegetation, but not at ground level. In captivity larvae spun cocoons among leaves of the host, and, like reared *H. c. gloveri*, in the lower folds of the sleeve.

Comparative Life History.—All members of *Hyalophora* are univoltine, with adults emerging in the spring in temperate regions. Southern Arizona populations of *H. c. gloveri* often emerge during the late summer monsoon season, sometimes preceded by a facultative partial emergence during spring rather than a true bivoltine flight (Tuskes et al., 1996). The adult flight season is short, usually lasting three to four weeks. Adult males are strong fliers, as shown in various dispersal studies (Collins, 1984). In mark-and-recapture studies using virgin females as bait, male *H. cecropia* commonly flew over 5 km over several nights and one male was taken 12.5 km from the point of release. The dispersal potential of females is not well known, as no reliable method for tracking or recapture is available. Newly mated females are heavily laden with ova, but may fly greater distances as they finish oviposition. Potential rates of gene flow must be high in *Hyalophora*, an important parameter in the formation and maintenance of hybrid zones.

The larvae of all species feed on shrubs and trees and mature in about six to eight weeks. With the important exception of northern populations of *H. c. columbia*, most populations of all taxa tend to be polyphagous (Table 8). Perhaps the most polyphagous species is *H. cecropia*, although this tendency may be exaggerated by its ability to thrive in suburban situations where the larvae feed on ornamentally planted shrubs and trees, including exotics (Scarbrough et al., 1974). Willows (Salicaceae), rosaceous shrubs and small trees, Ericaceae, and Rhamnaceae are common hosts shared by both *H. euryalus* and *H. c. gloveri*. These species differ in the acceptance of Douglas fir (*Pseudotsuga menziesii*) by *H. euryalus* and the use of Elaeagnaceae by *H. c. gloveri*. The northeastern populations of *H. c. columbia* appear to feed exclusively on larch or tamarack (*Larix*), a deciduous conifer, although populations in Manitoba and Ontario transitional to *H. c. gloveri* feed also on Betulaceae and various *Prunus* (Rosaceae) (Kohalmi and Moens, 1975, 1988).

The natural hosts of *kasloensis* are not well known. I collected two cocoons in the study area on western choke cherry (*Prunus demissa*), and reared stock (a minimum of three broods of 20–30 larvae each for each host plant) on this host and on *P. emarginata*, as well as on various *Ceanothus*, *Rhamnus rubra*, *Salix exigua* (a common willow host of *H. euryalus* and *H. c. gloveri*), and *Elaeagnus angustifolius*. Morewood (1991) reared British Columbia stock of *kasloensis* on *Ceanothus sanguineus*, *Rhamnus purshiana*, and *Pseudotsuga menziesii*. In addition, I have reared two broods from the same Okanagan Valley region on *Shepherdia argentea*. McGugan (1958) listed *Shepherdia canadensis* as a host for *H. euryalus*, and although he did not differentiate interior from coastal records, this shrub is confined largely to the drier interior where *kasloensis* occurs. Stock of *kasloensis* from Montana (four broods of 10–20 larvae each) refused to accept *Pseudotsuga*, and this trait may distinguish these populations from the *kasloensis* in British Columbia. Based on rearing experience and the distributions of potential hosts, it seems reasonable to include *Ceanothus*, *Rhamnus*, *Elaeagnus*, *Shep-*

Table 8.—*Host plants of* Hyalophora.

Species	Family of host plant							
	Rosaceae	Salicaceae	Rhamnaceae	Ericaceae	Elaeagnaceae	Pinaceae	Betulaceae	Aceraceae
H. cecropia[1]	*Prunus* *Malus*	*Salix*					*Betula*	*Acer*
H. euryalus	*Prunus* *Purshia* *Cercocarpus*	*Salix*	*Ceanothus* *Rhamnus*	*Arctostaphylos* *Arbutus*		*Pseudotsuga*	*Corylus*	
H. c. gloveri	*Prunus* *Purshia* *Rosa* *Cercocarpus*	*Salix*	*Ceanothus*	*Arctostaphylos*	*Elaeagnus*			
H. c. columbia[2]						*Larix*		

[1] *Hyalophora cecropia* has been recorded from many other hosts (e.g., Scarbrough et al., 1974) including exotic, ornamental *Rhamnus.*

[2] Larvae of *H. c. columbia* near the blend zone with *H. c. gloveri* in Ontario and Manitoba also feed on *Prunus* and Betulaceae.

herdia, *Salix*, and possibly *Pseudotsuga* as natural hosts of *kasloensis*. Western larch (*Larix occidentalis*) is common in the Bitterroots in areas where *kasloensis* has been collected, including at high altitudes where other potential hosts are scarce, but I have been unable to confirm this probable host nor have I attempted to rear larvae on it.

The hosts of the hybrid populations in the Boise, Idaho, region are not known, but *Prunus emarginata* is especially common where moths have been collected, and various willows and *Ceanothus velutinus* may also be natural host plants.

Morphometrics of Hybrid Populations

The discriminant functions generated from wing characters produced an accurate classification of reference groups (Table 9). All specimens in the *H. euryalus* reference sample were identified correctly, and only 9.7% were placed in class 2 (between *H. euryalus* and F_1 hybrids) when reclassified using Mahalanobis distances. The reference group for *H. c. gloveri* was placed correctly in *H. c. gloveri*, with the exception of one individual identified as an F_1 hybrid in the standard three-way classification. This specimen and two others were placed in class 4 based on distance values; two of the three were unusually small, and two of the three had some red scaling in the postmedial color band. Both of these traits occur occasionally in indisputably pure *H. c. gloveri* populations, but their coincidence in these specimens caused the misclassification. Predictably, the laboratory F_1 hybrids showed the most variability, although 93.4% were correctly identified in the standard classification, and 91.2% were in class 3 (F_1 hybrids) in the five-class scheme based on distance values. Accuracy of the classification of wild specimens was confirmed by the three nearly nonoverlapping clusters of scores for reference samples plotted on the first and second canonical variables (Fig. 2).

There is an obvious trend in phenotypic variability from essentially pure *H. c. gloveri* at the Continental Divide near Helena, Montana, and the Pony, Montana, population to nearly pure *H. euryalus* on the western slopes of Lookout Pass, Idaho. Intervening samples show a smooth intergradation, with the highest frequency of F_1 hybrid-like phenotypes near Missoula, Montana; 67.9% were classified as such in the standard classification, and 53.6% were placed in class 3 based on distances (Fig. 3). Individual specimens were placed in all classes except for class 5, pure *H. c. gloveri*. Among the samples, *H. euryalus*-like individuals are found near Missoula, Montana, and *H. c. gloveri*-like moths are found west of the Continental Divide (Fig. 5).

Another zone of intergrades was found northeast of Boise, Idaho, in the drainage system formed by Mores Creek Canyon and Clear Creek Canyon from Idaho City to Banner Summit (Table 9; Fig. 4, 5). This sample of 55 moths contained individuals in all phenotypic classes in both classification schemes, although 76.3% were classed as F_1 hybrids in the standard scheme, and 69.1% were placed in the corresponding class 3 based on distance scores. These moths have a larger forewing length on average than those from Missoula (56.6 vs. 54.0 mm), and many appear more brightly colored (Fig. 6). Pure *H. c. gloveri* is found approximately 40 km west of the Sun Valley/Ketchum area in the Sawtooth National Forest, but the few adults taken 30 km to the northwest in Atlanta appear to be intergrades.

A third area of intergradation was found in the vicinity of Lost Trails Pass, near the intersection of the Continental Divide and the Bitterroot range. Moths of

Table 9.—*Classification (number of specimens, percentage) of* Hyalophora *populations based on discriminant analysis of wing characters, with* H. euryalus, H. columbia gloveri, *and their F_1 hybrids as reference groups. Phenotypic classes derived from Mahalanobis distance values.*

	Three-way classification			Phenotypic class				
Sample groups (number)	*H. euryalus*	Hybrid	*H. c. gloveri*	1 *H. euryalus*	2	3 Hybrid	4	5 *H. c. gloveri*
1a. West Lookout Pass, Idaho (Sweadner specimens) (16)	12 75.0	4 25.0	0 0	9 56.3	4 25.0	3 18.2	0	0
1b. West Lookout Pass, Idaho (40)	20 50.0	20 50.0	0 0	15 37.5	5 12.5	20 50.0	0 0	0 0
2. East Lookout Pass, Montana (Sweadner specimens) (33)	20 60.6	13 39.4	0 0	14 42.5	8 24.2	11 33.3	0	0
3. West Lolo Pass, Idaho (8)	3 37.5	5 62.5	0 0	1 12.5	4 50.0	2 25.0	1 12.5	0
4. East Lolo Pass, Montana (30)	13 43.3	16 53.3	1 3.4	4 13.3	9 30.0	15 50.0	2 6.7	0
5. Missoula, Montana (28)	8 28.6	19 67.9	1 3.5	4 14.3	4 14.3	15 53.6	5 17.8	0
6. Bearmouth, Rock Creek, Montana (16)	1 6.2	5 31.3	10 62.5	0	1 6.2	5 31.3	0	10 62.5
7. Continental Divide (20)	0	0	20 100.0	0	0	0	2 10.0	18 90.0
8. Sula, Montana (11)	3 27.3	6 54.6	2 18.1	2 18.2	1 9.1	3 27.4	4 36.2	1 9.1
9. Gibbonsville, Idaho (21)	0 0	1 4.8	20 95.2	0	0	1 4.7	2 9.6	18 85.7
10. Pony, Montana (22)	0 0	0 0	22 100.0	0	0	0	0	22 100.0

Table 9.—*Continued.*

Sample groups (number)	Three-way classification			Phenotypic class				
	H. euryalus	Hybrid	*H. c. gloveri*	1 *H. euryalus*	2	3 Hybrid	4	5 *H. c. gloveri*
11. Mores Creek Canyon/Clear Creek Canyon, Boise County, Idaho, hybrid zone (55)	3 5.5	42 76.3	10 18.2	3 5.5	2 3.6	38 69.1	6 10.9	6 10.9
F_1 = *H. kasloensis* female (Ravalli County, Montana) × *H. c. gloveri* male (Lemhi County, Idaho) (13)	0 0	10 83.3	2 16.7	0 0	0 0	3 25.0	8 66.7	1 8.3
F_1 = *H. euryalus* female (Nevada County, California) × *H. kasloensis* male (Missoula County, Montana) (13)	11 84.6	2 15.4	0 0	4 30.8	7 53.8	2 15.4	0 0	0 0
F_1 = *H. c. columbia* female (Ontario, Canada) × *H. kasloensis* male (Ravalli County, Montana) (6)	0 0	2 33.3	4 66.7	0 0	0 0	2 33.3	2 33.3	2 33.3
Reference *H. columbia gloveri*: Boulder, Colorado (33)	0 0	1 3.0	32 97.0	0 0	0 0	0 0	3 10.0	30 90.0
Lab Reference F_1 hybrids: *H. euryalus* × *H. c. gloveri* (45)	3 6.7	39 86.7	3 6.7	2 4.4	0	41 91.2	1 2.2	1 2.2
Reference *H. euryalus*: northern California (31)	31 100.0	0 0	0 0	28 90.3	3 9.7	0	0	0

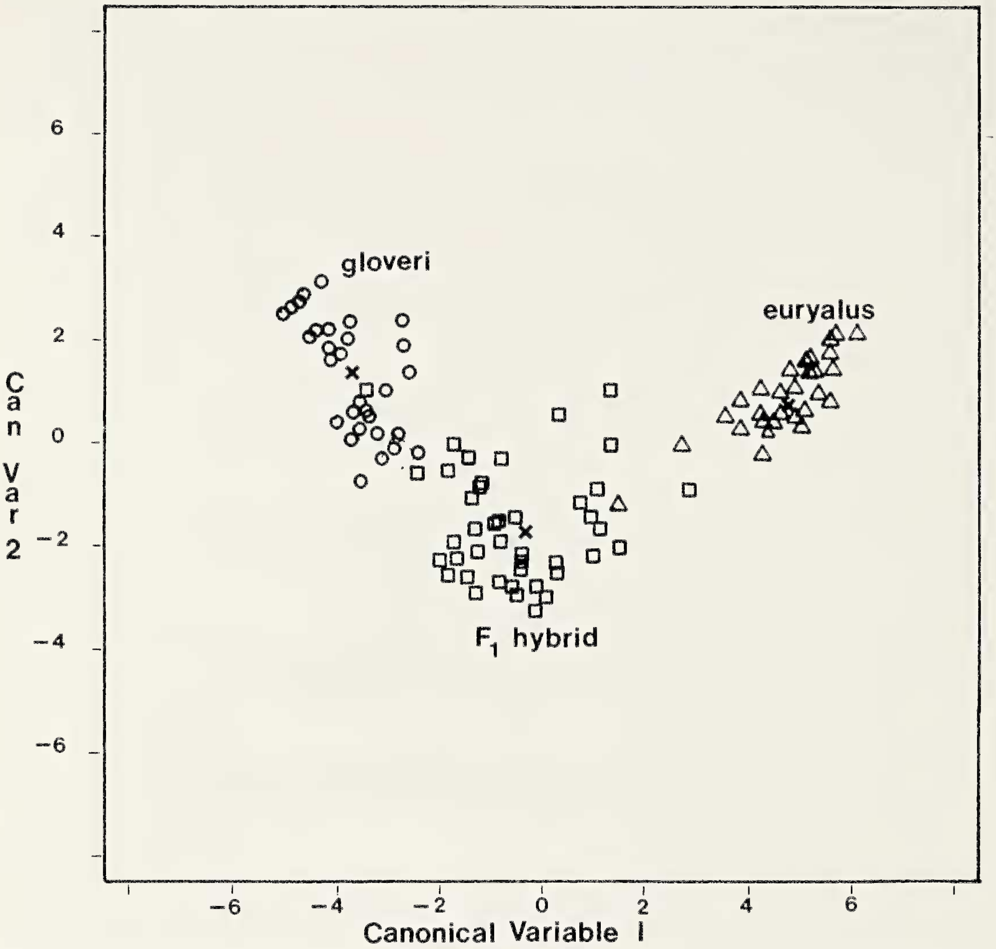


Fig. 2.—Scatter diagram of canonical variable scores from discriminant analysis of adult phenotypes from reference populations: *Hyalophora columbia gloveri*, *H. euryalus*, and their laboratory F_1 hybrids. X = group centroid.

the *kasloensis* phenotype (taken near Missoula) are found in Sula, just north of the pass, but nearly pure *H. c. gloveri* are found south over the pass near Gibbonsville, Idaho. However, three out of 21 males showed intermediate characters; one was placed in class 3 and two in class 4. The entire distribution of *Hyalophora* in western North America is shown in Figure 7.

DISCUSSION

Hybrid Origin of kasloensis *and Other Intergrade Populations*

Data gathered from morphometric analysis, examination of immature stages, experimental hybridization, and biogeography all support a hybrid origin of *Hyalophora* populations from the Bitterroot Mountains, referred to here as *kasloensis*. The geographic pattern of adult phenotypic variation corresponds to a hybrid zone and a majority of specimens were classified as hybrids using reared F_1

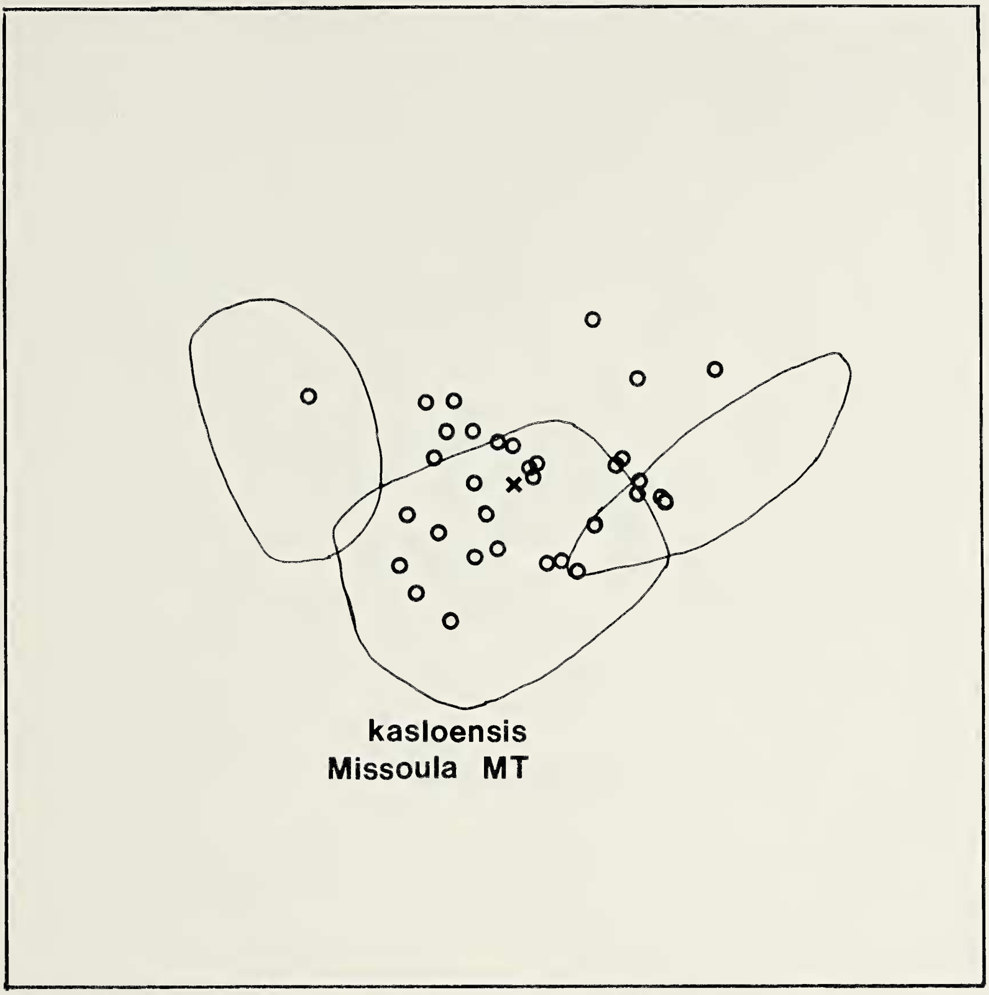


Fig. 3.—Scatter diagram of discriminant analysis scores of the Missoula, Montana, *Hyalophora* "*kasloensis*" sample population (Table 9). Distribution of reference sample scores shown in outline. X = group centroid.

hybrids as a reference series. Character clines exist that suggest hybridization and introgression, from *H. euryalus*-like phenotypes to the west to *H. c. gloveri*-like phenotypes in the east; this is especially apparent for the shape of the hindwing discal spot (Fig. 8). The first through fourth instars of *kasloensis* resemble *H. c. columbia* or *H. c. gloveri* more than corresponding instars of *H. euryalus*. The red to orange coloration of dorsal scoli in the final instar is unique to *kasloensis*, although the dorsal thoracic scoli of *H. c. columbia* are red. In fourth instars of *H. c. gloveri*, all dorsal scoli may be reddish, and perhaps in the mature *kasloensis* larva a disruption of gene regulation maintains the expression of this pigment into the next instar. A wide range of developmental incompatibilities are known in hybrids of Lepidoptera (Oliver, 1979, 1980) and of other organisms (Berven and Gill, 1983; Woodruff, 1989). Hybrid larvae reared from *H. euryalus* × *H. c.*

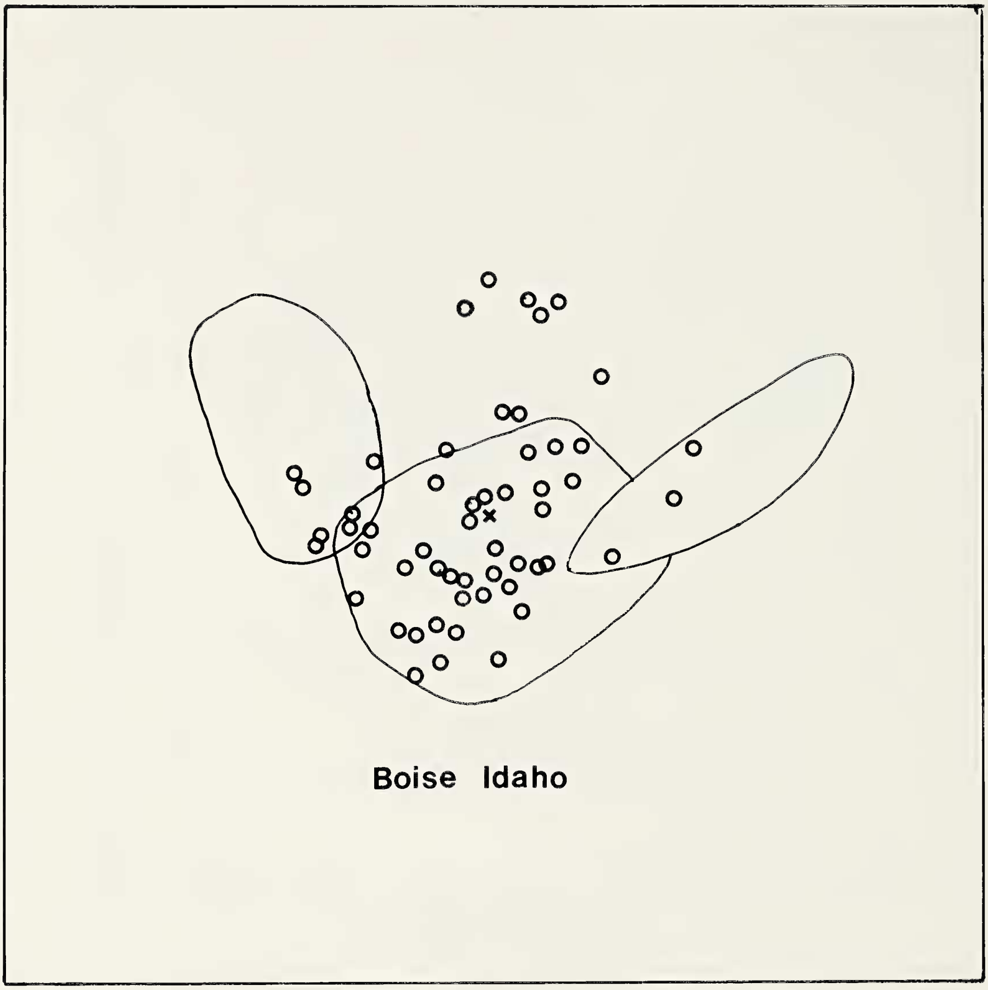


Fig. 4.—Scatter diagram of discriminant analysis scores of the Boise, Idaho, *Hyalophora* hybrid population. Distribution of reference sample scores shown in outline. X = group centroid.

gloveri crosses all had yellow dorsal scoli in the last instar; I have no data on larval coloration in *H. euryalus* × *H. c. columbia* larvae. The cocoon of *kasloensis* is intermediate in shape and texture between *H. euryalus* and *H. c. gloveri.*

Significant reproductive incompatibility occurred in experimental crosses between *kasloensis* and both *H. euryalus* and the subspecies of *H. columbia.* This incompatibility was expressed in fertility, viability, and sex ratios of F_1 broods for at least one of the reciprocal crosses between *kasloensis* and the other taxa. The genetic compatibility in hybrids between *H. euryalus* and *H. c. gloveri,* including stock bordering the California Sierra Nevada hybrid zone, was much higher than for hybrid crosses between *kasloensis* and the two latter species. Hybrid unfitness in crosses between *H. euryalus* and *H. c. gloveri* is usually associated with F_1 hybrid female sterility, but ova hatch rates and adult sex ratios are normal (Collins, 1984). Compatibility between *kasloensis* and *H. euryalus*

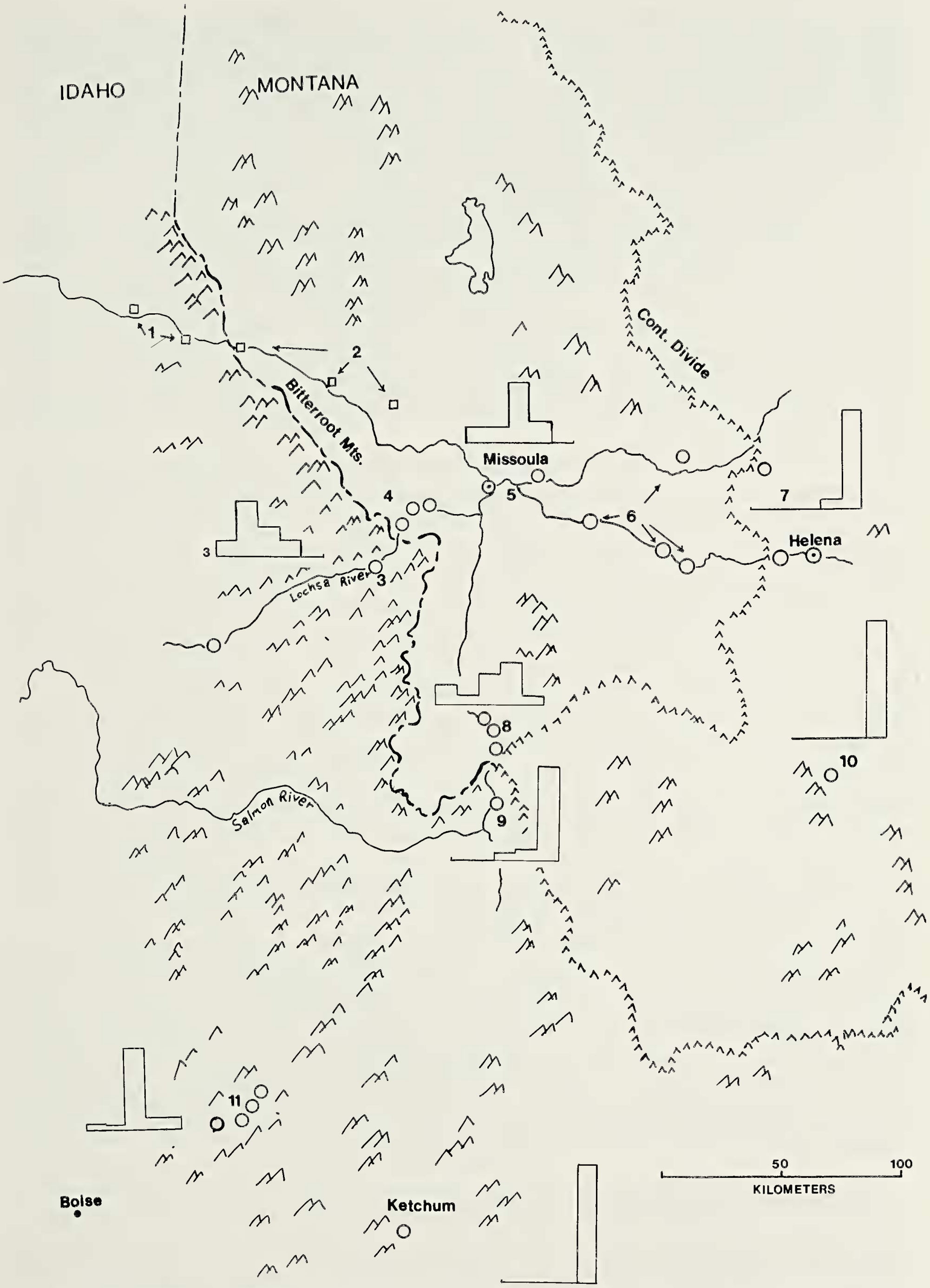


Fig. 5.—Geographic distribution of adult phenotypes for the Bitterroot Range *Hyalophora* hybrid zones. Phenograms based on discriminant analysis scores plotted as five classes from pure *H. euryalus* (left) to pure *H. c. gloveri* (right). Site numbers correspond to those listed in Table 9. Phenotypes collected near Ketchum, Idaho, appear to be pure *H. c. gloveri*; sample too small for analysis.

was variable, with certain crosses expressing a low fertility rate (Table 1:group III, crosses 2, 5) and others a low viability (Table 1:group IV, cross 1), but in general the compatibility with *H. euryalus* was higher than that seen in crosses between *kasloensis* and *H. c. gloveri* (Table 1:groups VII, VIII). Both fertility and viability were depressed in several such crosses involving female *H. c. gloveri.*

If genetic compatibility is taken as a measure of genetic similarity, then *kasloensis* would be seen as genetically distinct from *H. euryalus* and even further removed from *H. c. gloveri,* using experimental interpopulation crosses within these two species as a standard of comparison. Results of experimental hybridization do not support considering *kasloensis* to be a subspecies of *H. euryalus,* but instead point to a significant degree of developmental incompatibility in hybrid crosses between *kasloensis* and all other *Hyalophora*; a ranking by increasing incompatibility would be *H. euryalus, H. c. columbia,* and *H. c. gloveri.* In addition, a significant incompatibility was found in crosses between distant populations of *kasloensis,* indicating a degree of geographic genetic differentiation not found in other *Hyalophora.*

The clinal variation in the *kasloensis* adult phenotype revealed by morphometric analysis theoretically could result from either primary or secondary intergradation (Endler, 1977). The geographic location of the zone is consistent with a secondary contact resulting from a postglacial recolonization from refugia in the Sierra Nevada (*H. euryalus*) and from the Southwest and southern Rocky Mountains (*H. columbia*). Morphometric analysis of the Boise intergrade zone strongly suggests a hybrid origin for this population as well (Table 9). In a preliminary allozyme survey of the Sierra Nevada hybrid zone, Collins et al. (1993) found polymorphism in nine of 20 loci tested; the genetic identity index between *H. euryalus* and *H. c. gloveri* was 0.932. Clines across the hybrid zone in frequencies of nonfixed alleles corresponded to expectations based on gene flow. One locus was fixed for alternative alleles in *H. euryalus* vs. *H. c. gloveri,* with heterozygotes present only in the hybrid zone. A sample of six adults from the Boise population was also heterozygous for this locus, corroborating the proposed hybrid origin for this population. No comparative data were available on the allozyme composition of adjacent parental populations, and a comprehensive survey of all these Pacific Northwest populations is pending.

The presence of hybrid zones (indicating a degree of reciprocal gene flow in parapatry) and the genetic compatibility seen in experimental hybridization (Table 1) would support a closer relationship between *H. euryalus* and *H. c. gloveri* than between either of these species and *H. cecropia* (Table 7). Compared to crosses of *H. euryalus* × *H. c. gloveri,* premating isolation and postzygotic barriers are more effective in hybrid crosses between *H. cecropia* and its congeners, and extensive hybridization does not occur in nature in areas of sympatry between *H. cecropia* and the subspecies of *H. columbia.*

Experimental Hybridization, Phylogenetic Inference, and Species Limits

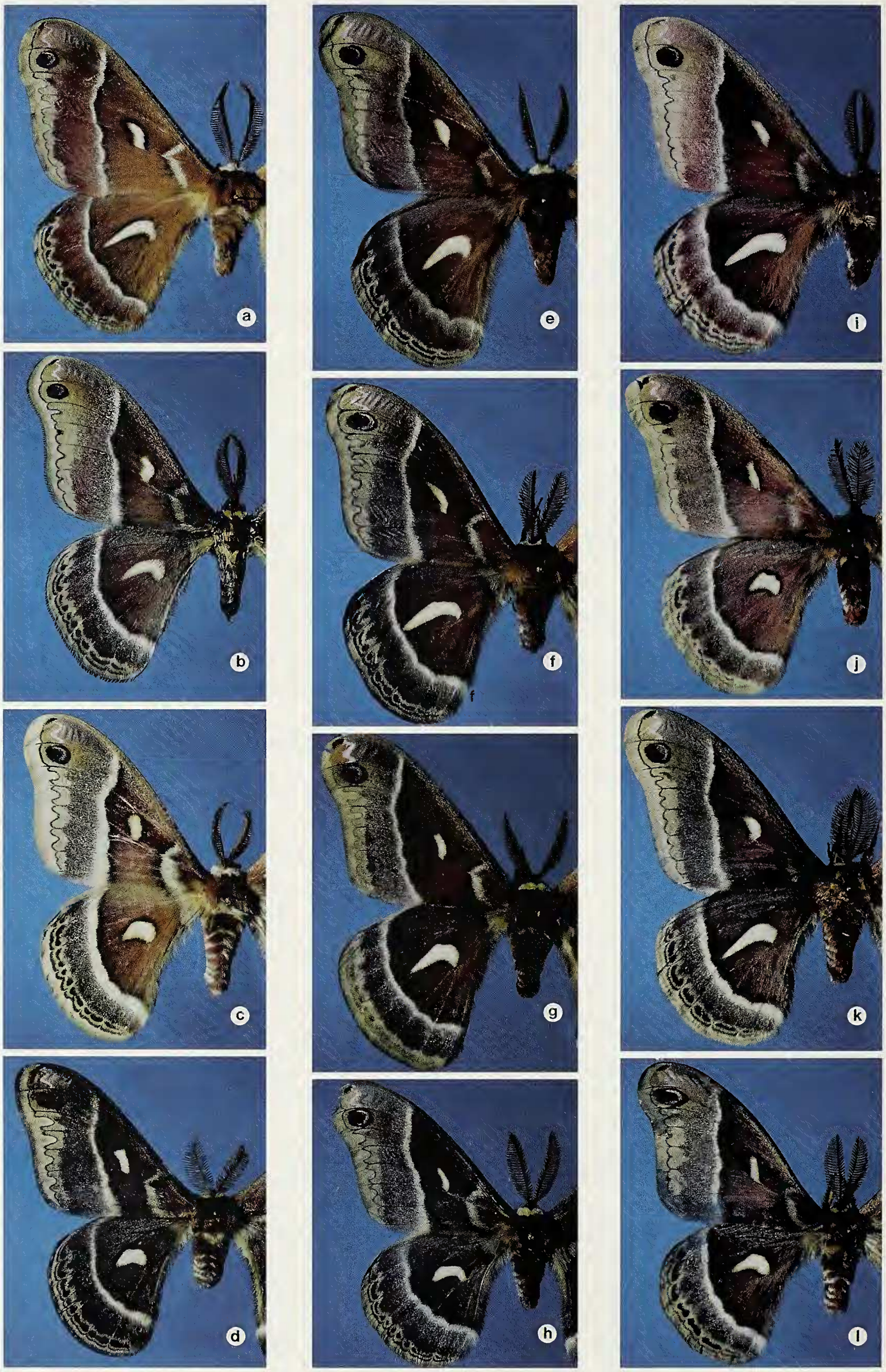
Experimental hybridization, as a means of measuring reproductive and developmental compatibility, traditionally has been employed to investigate taxonomic relationships, both at the species level and above (Remington, 1958). Even with the development of molecular techniques in genetic analysis, laboratory hybridization remains the most effective technique to reveal differences in genes controlling reproductive isolation among closely related species (Templeton, 1981).

Recently, however, reproductive compatibility has been considered to be a shared, ancestral trait among closely related taxa and therefore inappropriate for use in phylogenetic inferences (Cracraft, 1983, 1989; Zink, 1988; Frost and Hillis, 1990). Moreover, practical difficulties arise in entering hybrid character data into cladistic analysis due to the intrinsically reticulate nature of hybrid phenotypes (Wagner, 1983; McDade, 1992). Degree of postzygotic isolation may not indicate species relationships reliably. Hillis (1988) recognized several new species of leopard frogs (*Rana*) on the basis of mating-call differences in sympatric populations, morphology, and allozyme studies. The majority of interspecific crosses produced offspring capable of metamorphosis, but in virtually all cases the hybrid progeny showed some reduction in fitness. This reduction in fitness was not well correlated with phylogenetic relationship inferred from allozyme analysis. Morphological evolution is conservative among the leopard frogs, and hybrid compatibility often showed a correlation with adaptation to similar ecological conditions during development, even in crosses between species judged otherwise to be distantly related.

An opposing point of view holds that postzygotic barriers may arise incidental to genetic changes during speciation, and that such traits are useful in systematics because they reflect the history of genetic divergence of the taxa in question, and directly affect the potential of previously allopatric populations to maintain genetic integrity upon secondary contact (Templeton, 1989; Avise and Ball, 1990; Highton, 1990, 1995). These authors cite the extensive data on the genetics of species differences in *Drosophila*, as discussed by Orr (1987) and Coyne and Orr (1989*a*, 1989*b*). Male hybrid sterility typically is produced by incompatibility in gene action between loci on the X chromosome and autosomes, and female sterility is due largely to disruption of X chromosome–cytoplasm interaction. With increasing phylogenetic distance between the *Drosophila* parent species, the fitness of their hybrid progeny gradually decreases. A similar correlation between genetic incompatibility and phylogenetic distance, although less well documented, appears to be true for Lepidoptera (Oliver, 1979, 1980; Lorković, 1985; Collins, 1991; Ae, 1995).

By the "recognition species concept" (Paterson, 1985), the entire *Hyalophora* assemblage could be considered a single species, although this viewpoint would ignore obvious phenotypic, genetic, and ecological differentiation. Avise and Ball (1990) described a species concept incorporating aspects of both the phylogenetic concept (Cracraft, 1983) and species concepts based on genetic cohesion among component populations of a species (e.g., Templeton, 1989; Mallet, 1995). Avise and Ball (1990) review methods for determining "genealogical concordance" by inferring phylogeny from geographical patterns of gene sequences (e.g., mtDNA). Like the phylogenetic species concept, this approach seeks to determine ancestor–descendant lineages, but it also recognizes the importance of reproductive isolation to genetic and phylogenetic divergence.

Hyalophora in many ways are especially suitable for experimental measurement of genetic cohesion with respect to species limits. Data on genetic compatibility, available from laboratory pairings and analysis of natural hybrid zones, can provide an estimate of genetic cohesion within groups defined by other measures, such as geographic patterns in morphological or molecular characters. Hybrid zones are evidence of significant phylogenetic divergence between taxa and are maintained by barriers to gene flow due to hybrid incompatibility at critical loci. In *Hyalophora* the underlying fitness loci appear to regulate oögenesis. Careful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genetic analysis of hybrid zones can potentially reveal the basis of discontinuities in genetic cohesion among closely related taxa (Mallet and Barton, 1989*a*, 1989*b*; Sperling and Spence, 1990; Sperling, 1993*a*; Hagen and Scriber, 1995), which can be compared with phylogenetic hypotheses derived from independent data sets. Correlations between genetic discontinuity and phylogenetic relationships may reveal the pattern of divergence during speciation for genes regulating postzygotic compatibility.

Sterility in hybrids, skewed sex ratios, and other abnormalities confined to one sex are all examples of "Haldane's rule," the predominant expression of hybrid unfitness in the heterogametic sex. In a model proposed by Coyne and Orr (1989*a*), recessive alleles that are beneficial accumulate through mutation at loci on the sex chromosomes. In the heterogametic sex (females in Lepidoptera), these alleles pleiotropically interact with autosomal genes to regulate the expression of sex-related traits such as those associated with reproduction. Gene expression in hybrids of the heterogametic sex is disrupted, producing inviability, sterility, or other abnormalities. This model both explains the basis of single-sex hybrid unfitness and provides testable hypotheses of genetic divergence during speciation. In a companion study of speciation patterns in *Drosophila*, Coyne and Orr (1989*b*) concluded that newly diverged taxa produce sterile or subvital male hybrids (the heterogametic sex), but that female sterility evolves at a slower rate. Hagen and Scriber (1995) interpreted their extensive study of speciation in the tiger swallowtail butterflies (*Papilio*) in terms of these models and found an overall agreement with predictions for inheritance patterns of diapause problems and distorted sex ratios in hybrids; sex-linked species differences may be common in Lepidoptera (Sperling, 1994). Orr (1995) presented a mathematical model of speciation based on homologous loci in diverging taxa in which derived alleles produce incompatibility in hybrid genomes. This model predicts an increase in probability of speciation (postzygotic isolation) at a rate much faster than linearly with time. These results also predict that postzygotic isolation may arise sooner than either prezygotic isolation or divergence in traditional morphologic taxonomic characters.

Female sterility in interspecific *Hyalophora* hybrids is widespread, but hybrids are viable and developmental incompatibility typically is not severe. Interspecific female hybrids among the closely related *Callosamia* also are sterile, and inviability and developmental abnormalities are more severe than within *Hyalophora* (Haskins and Haskins, 1958; Peigler, 1977). Female sterility is the rule in other saturniid hybrids (Tuskes et al., 1996), even in hybrids between the semispecies

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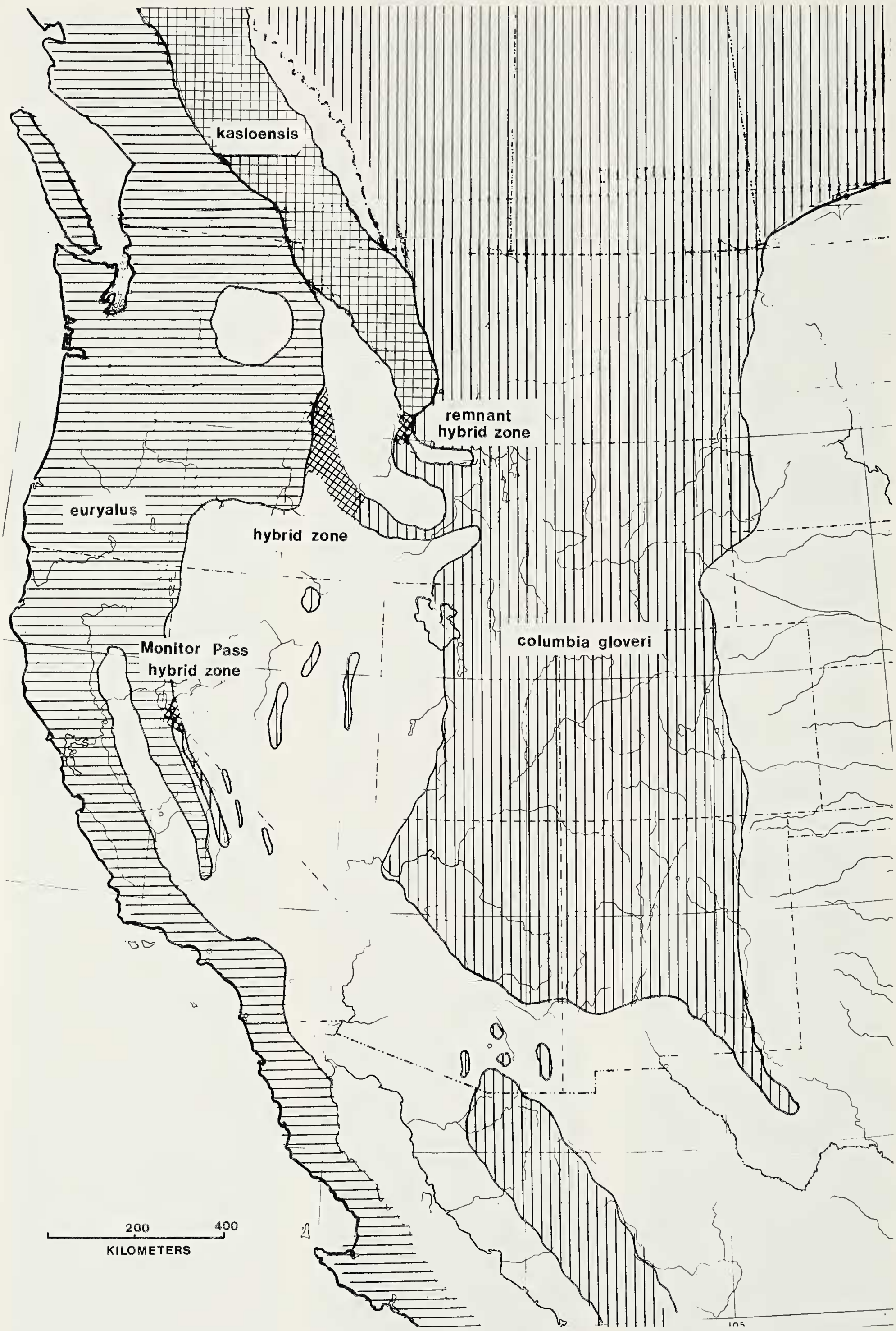
Fig. 6.—Variation in *Hyalophora* adult phenotypes. a, *Hyalophora euryalus*. California, Siskiyou County, 3 mi E McCloud, 3 July 1971. b, F_1 hybrid = *H. euryalus* ♀ California, Ventura County, Mulholland Canyon × *H. columbia gloveri* ♂ Nevada, Elko County, Ruby Mountains, ecl. 16 May 1992. c, *Hyalophora columbia gloveri*. Montana, Madison County, S Pony, Tobacco Root Mountains, 15 June 1983. d, *Hyalophora c. columbia*. CANADA, Manitoba, 13 mi W Braintree, 15 June 1966. e–h, *Hyalophora "kasloensis."* e, Idaho, Idaho County, Wildgoose Campground, 20 mi E Kooskia, 9 June 1989; f, Montana, Missoula County, Bearmouth, 9 June 1989; g, Montana, Missoula County, 3 mi E Milltown, 10 June 1989; h, Montana, Missoula County, Rock Creek, 8 June 1989. i–l, *Hyalophora* hybrid intergrades. i, Idaho, Boise County, 25 mi N Idaho City, 10 June 1993; j, Idaho, Boise County, 12 mi N Idaho City, 10 June 1993; k, Idaho, Boise County, 14 mi N Idaho City, 10 June 1993; l, Idaho, Boise County, 25 mi N Idaho City, 10 June 1993. All specimens males, × .60; to caged females (except b).


kasloensis
remnant hybrid zone
euryalus
hybrid zone
Monitor Pass hybrid zone
columbia gloveri
200
400
KILOMETERS
105

Saturnia mendocino and *S. walterorum* (Tuskes and Collins, 1981). By circumventing natural mating barriers, breeders of saturniids have produced various intergeneric hybrids that show predictably increased developmental incompatibility (Peigler, 1978; Carr, 1984; Weast, 1989; Tuskes et al., 1996). In spite of losses due to hybrid unfitness, the successful production of any such intergeneric hybrids is evidence that the genes controlling basic morphogenesis are fundamentally similar in these genera, and therefore are evolutionarily conservative. In hybrids between the North American *Callosamia* and Asian *Samia*, phenotypes of larvae, cocoons, and adults are not distorted or disrupted, but often are strikingly intermediate in comparison to the differences between the parental species. By contrast, hybrid female sterility appears to be the most widespread manifestation of genetic incompatibility in interspecific hybrids in the Saturniidae and in other Lepidoptera families. This pattern suggests that developmental incompatibility, especially for genes controlling oögenesis, derives either from genetic differentiation during the speciation process or shortly thereafter. Progressively more severe disruption of development is seen as phylogenetically more distant taxa are crossed.

Pleistocene Environments and the Origin of Hyalophora *Hybrid Zones*

Climatic changes during the Pleistocene obviously had a profound effect on the distribution and abundance of organisms, and consequently also influenced genetic differentiation and speciation (Vrba, 1985; Hewitt, 1993). Lepidoptera leave very few fossils, with none known from the Quaternary, so that biogeographic and phylogenetic inferences must be made from living forms and from the fossil remains of their modern host plants (e.g., Tuskes and Collins, 1981). Even assuming that present-day host plants reflect ancient associations, inferring historical range changes in the *Hyalophora* from fossil plant remains is made more difficult by the polyphagy of the various species. Consequently, in the following discussion I assume a degree of polyphagy for the progenitors of modern *Hyalophora* taxa. All recognized species are to varying degrees ecological generalists, and throughout their ranges occupy a wide variety of climates and plant communities.

During the Cenozoic Era a warm, moist climate prevailed in North America and, until the Rocky Mountains formed late in the era, a tropical flora occupied a vast area with little east-to-west differentiation (Daubenmire, 1975; Mathews, 1979). Miocene fossils in northern Idaho and eastern Washington show remnants of a mixed forest of temperate deciduous trees combined with a few evergreen angiosperms, such as *Arbutus*. During this time many tree species disappeared, including *Juglans*, *Liquidambar*, *Sassafras*, and *Magnolia*. The Madro–Tertiary flora evolved as xeric-tolerant sclerophylls, probably first appearing in the lee of the mountain ranges then forming (Axelrod, 1977). During the Miocene this flora occupied much of California and central Nevada. The Madro–Tertiary flora was displaced toward the West Coast as the climate became cooler and drier, producing the oak–madrone woodland and chaparral communities now widespread in Cali-

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Fig. 7.—Geographic distribution of *Hyalophora* in western North America. Based on the author's collecting records, published records (Peigler and Opler, 1993; Tuskes et al., 1996), and on estimations derived from host plant associations.

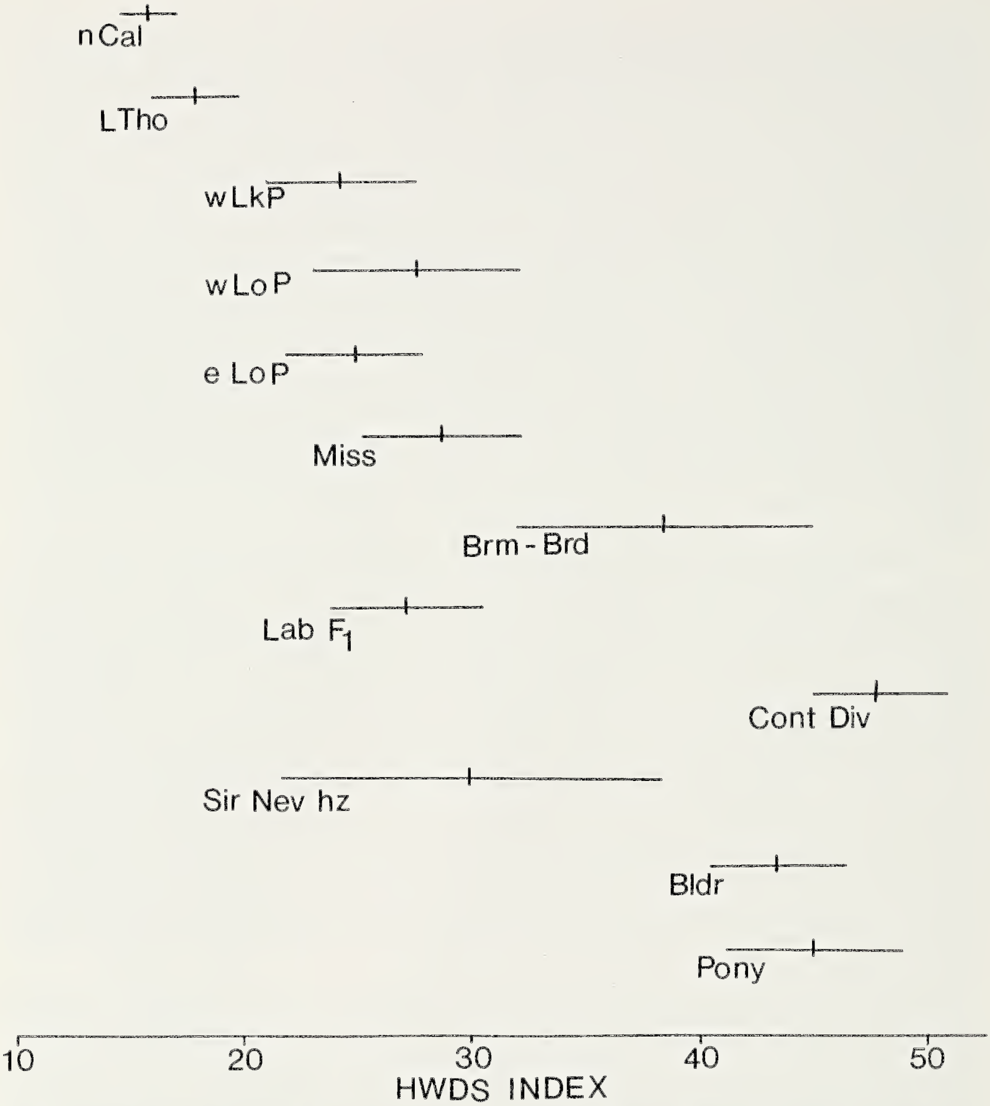

Fig. 8.—Phenotypic structure of the *Hyalophora "kasloensis"* hybrid zone and reference populations as shown by variation in the hindwing discal spot shape; mean and SD. Pure *H. euryalus*: northern California (nCal), Lake Tahoe (LTho); *H. kasloensis*: west Lookout Pass (wLkP), west Lolo Pass (wLoP), east Lolo Pass (eLoP), Missoula (Miss), Bearmouth to Brandon (Brm–Brd); laboratory F_1 hybrids (Lab F_1); pure *H. columbia gloveri*: Continental Divide (Cont Div), Sierra Nevada hybrid zone (Sir Nev hz), Boulder, Colorado (Bldr), Pony, Montana (Pony); Monitor Pass. Localities as listed in Table 9 and see Figure 5 for distribution of adult phenograms.

fornia. Another remnant of this once widespread flora is the evergreen oak woodland (associated with manzanita and madrone) now found in Arizona and the Sierra Madre of Mexico.

The family Saturniidae probably arose in the tropics of the New World, the region where the greatest saturniid diversity is found and where the more primitive saturniid genera and families most closely allied with the saturniids occur (Michener, 1952; Lemaire, 1978; Tuskes et al., 1996). The saturniids apparently emigrated to the Old World, diversified, and reinvaded the New World, probably across the Bering land bridge connecting Asia with North America (Ferguson, 1971). The genera *Saturnia*, *Actias*, and *Antheraea* are diverse in the Old World, but each are represented by only a few species in the New World. The genus *Hyalophora* is found only in North America.

Many Lepidoptera fossils in the Oligocene Florissant shales appear to belong to modern genera (Emmel et al., 1992), and the antiquity of modern genera or even species may be generally true for other insect orders (Elias, 1994). Given the apparently conservative rate of evolution in the Lepidoptera, it seems reasonable to assume that the genus *Hyalophora* probably arose in the Cenozoic in North America. At the beginning of the Pleistocene, the *Hyalophora* may have consisted of three elements: the respective ancestors of *H. cecropia*, *H. columbia*, and *H. euryalus*. *Hyalophora cecropia*, or its immediate ancestor, probably evolved in the eastern deciduous woodland in association with many plant families in this center of plant diversity. The common ancestor of *H. columbia* and *H. euryalus* must have evolved in association with the Madro–Tertiary geoflora, with their larvae feeding on sclerophylls such as *Ceanothus*, *Rhamnus*, and *Arctostaphylos*. As the Rocky Mountains arose, the moths expanded their host range to include willow and various *Prunus* species. As the climate changed late in the Tertiary the *Hyalophora* became divided into a West Coast element (giving rise to *H. euryalus*) and a Rocky Mountain and Great Basin element (the ancestor of *H. columbia gloveri*).

The following summary of the last North American interglacial period (Sangamon), the final stage of glaciation (Wisconsin), and the postglacial Holocene is based largely on reviews by Wright and Frey (1965), Butzer (1971), Mathews (1979), Thompson (1988), and Pielou (1991). The climate during the Sangamon interglacial (ca. 80,000–70,000 YBP) is thought to have been somewhat warmer and wetter than at present, with a northward shift in the ranges of many tree species, and the distribution of *Hyalophora* in the Great Basin was probably more extensive.

The continuity of Cordilleran glacier complex in the west with the Laurentide ice sheet to the east is uncertain (Fig. 9), but the former was not directly connected to the glaciers present in the Cascade/Sierra Nevada ranges or with those in the Rocky Mountains. A cold, dry, windswept, treeless grassland steppe evidently occupied the lower elevations in the Great Basin, Rocky Mountains, and western Great Plains and much of the Great Plains and the Mississippi Valley was covered with windblown soil and sand. The Pleistocene and early Holocene flora of the Great Basin and desert Southwest has been reconstructed in great detail from examination of fossil pack rat middens (Van Devender, 1977; Van Devender and Spaulding, 1979), supplementing earlier work with fossil pollen records (Martin, 1963; Martin and Mehringer, 1965). During the Pleistocene the Great Basin was not invaded by alien tree species from either the Cascades or the Rockies, but rather the upper altitude limits of various plant zones shifted to lower elevations. A pine parkland was found in much of the Southwest, with pinyon–juniper woodland at comparatively lower elevations in much of the southern Great Basin, and the Mojave and Sonoran deserts. True desert probably was confined to the region of the Colorado River in southern California and adjacent Arizona, separated from the pinyon–juniper woodland by a band of sagebrush scrub and chaparral. Pine

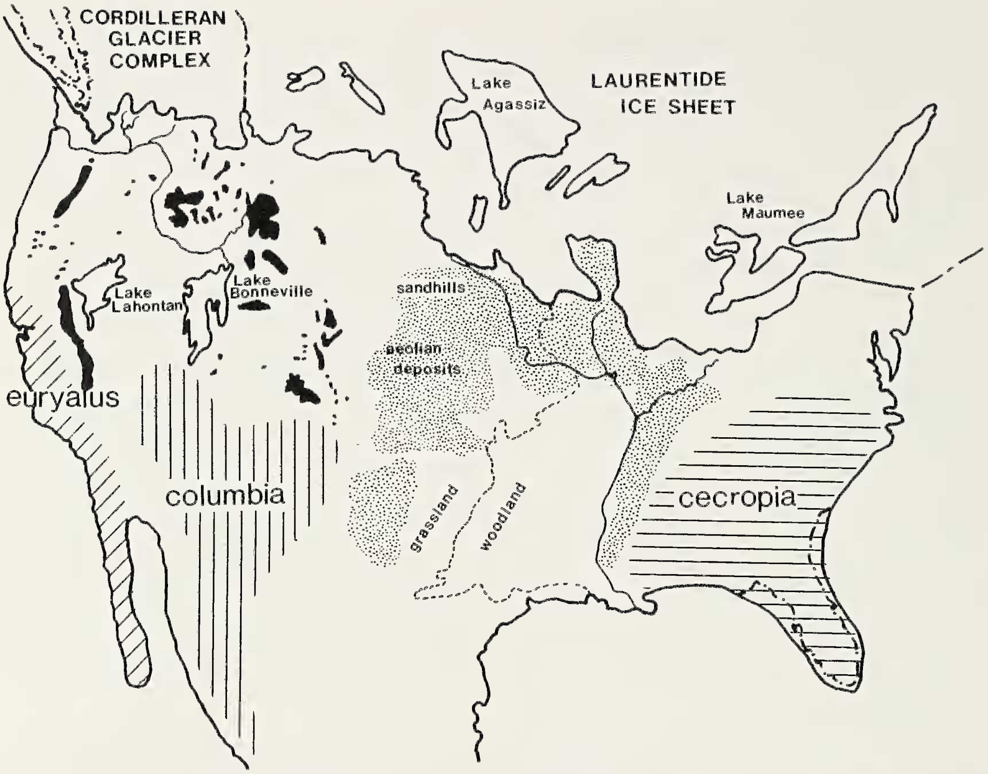

Fig. 9.—Hypothetical Pleistocene distribution of *Hyalophora* in North America during the Wisconsin stage of maximum glaciation. Geographic features based largely on Butzer (1971:fig. 57). Moth distribution based on paleobotanical and paleoclimatical data as cited in text.

forests mixed with scattered deciduous trees occupied the Southeast (Watts, 1980), grading into a spruce forest to the north. The West Coast south of the glaciers supported pine forests, with extensive glaciers forming in the High Sierra.

During the Wisconsin glacial maximum, *Hyalophora* probably would have been excluded from all but the southern extent of the present distribution. Populations of *H. euryalus* probably had an extensive distribution at low elevations in California and extending into Baja California. *Hyalophora c. gloveri* must have been restricted to the pinyon–juniper woodland of the Southwest and the southern Rocky Mountain region and isolated from *H. cecropia* by extensive dry grasslands and sandy regions to the east.

The recolonization of glaciated North America did not occur as a sequential northward movement of modern plant communities (Pielou, 1991). The rate of advance of each species depended on many factors including rates of seed dispersal, physiological tolerance, competitive interaction with other species, and distance from refugia. Some of the floral communities formed during postglacial times have no modern counterpart. Generally conifers invaded first, followed by a northward advance of deciduous hardwoods. As early as 14,000 YBP, shrubs colonized the grassland steppe bordering the retreating glaciers, and included the *Hyalophora* host plants silverberry (*Elaeagnus*) and buffalo berry (*Shepherdia*), and true willow (Lichti-Fedorovich, 1970). By 11,000–12,000 YBP, a spruce–

poplar–aspen forest had displaced this grassland, followed by birch, elm, ash, oak, and, lastly, pine. Many proglacial rivers and lakes were produced from melting ice, including those formed from buried ice; the latter are now the sites of prairie pot holes. A spruce–tamarack (*Larix*) muskeg formed in these mesic sites, much farther south than at present (Watts and Bright, 1968).

As the climate warmed these areas became warmer and drier and witnessed a sequence of changing forest flora: first balsam fir, then paper birch, white elm, burr oak, and finally (at about 8,000 YBP) the modern grassland of the Great Plains. To the east the retreating spruce forest was replaced sequentially by forests composed largely of jack pine, red pine, eastern white pine, firs, and finally by a mixture of paper birch, elm, and oak. In the west, lodgepole pine occupied a distribution corresponding to the eastern spruce forests, and was replaced by Douglas fir as the climate ameliorated (Axelrod and Ting, 1961; Axelrod, 1966; Baker, 1983).

The first *Hyalophora* colonizers east of the Rocky Mountains may have fed on the willows and Elaeagnaceae (*Elaeagnus*, *Shepherdia*). This association is now restricted to the Canadian Prairie Provinces, and it seems possible that the growing season may have been adequate to allow larval development at this early period preceding the plant succession that replaced the grassland steppe with forests. These *Hyalophora* populations subsequently may have adapted to feeding on *Larix* as the extensive spruce–tamarack bog/muskeg formed in the northern Great Plains. A brief period of warm climate, the Hypsithermal, occurred at about 8000 YBP, generally pushing plant communities northward and toward higher elevations in montane regions. The drying effect of the Hypsithermal was most severe in the rainshadow of the Rocky Mountains, where the modern prairie first developed and subsequently spread eastward. The present populations of larch-feeding *H. c. columbia* east of the Great Lakes probably represent a remnant of a much wider distribution, and may have been isolated from the larger subspecies *H. c. gloveri* by the spread of dry grasslands during the peak of the Hypsithermal.

Pioneer populations of *H. euryalus* probably exploited the northward movement of Douglas fir to colonize the coastal Northwest. Populations of *H. c. columbia* may have fed on western larch in the northern Rockies and hybridized with the conifer-adapted *H. euryalus* in the Bitterroot Range as both populations spread northward. *Hyalophora c. columbia* may have been displaced by *H. c. gloveri* from the south as hosts of the latter, such as *Prunus* and *Ceanothus*, became established in the northern Rockies. The present contact between the hybrid *kasloensis* populations and *H. c. gloveri* would then be secondary to the original hybridization event between *H. euryalus* and *H. c. columbia*. The rainshadow east of the Bitterroots must have been more severe during the Hypsithermal, perhaps isolating *kasloensis* from the *H. c. gloveri* east of the Continental Divide. Trapping data indicates that the density of *Hyalophora* and their hosts (except in riparian areas) decreases to the east of Missoula, which may explain the abrupt transition from the *kasloensis* phenotype to *H. c. gloveri* near the Continental Divide. The high Canadian Rockies appear to isolate *H. c. gloveri* from *kasloensis* to the west in the interior of British Columbia. During the Hypsithermal the grasslands of southeastern Washington and northeastern Oregon were probably more extensive and may have restricted gene exchange between *kasloensis* and *H. euryalus*. Antelope bitterbrush (*Purshia*) invaded the dry interior of British Columbia, Washington, and Oregon during this time (Daubenmire, 1969). Today this *Hyalophora* host is most common on the east slopes of the Cascades, but its historical distribution probably was never extensive enough to provide a corridor between lower elevation populations of *H. euryalus* to the *kasloensis* in the Bitterroots.

The hybrid zone near Boise, Idaho, probably formed as *H. euryalus* invaded eastward from the Pacific Northwest toward present-day Coeur d'Alene, Idaho, then migrated southward along the western slopes of the Bitterroots. These populations would have been confined to a narrow band, bordered by the dry grasslands to the west, a restriction magnified by the Hypsithermal event. These *H. euryalus* populations would have met and hybridized with *H. c. gloveri* (then expanding north from the southern Rockies) but would have remained isolated from *kasloensis* by the high mountain ranges in southern Idaho.

A shift of plant communities to higher elevations during the Hypsithermal probably produced a period of hybridization between *kasloensis* and *H. c. gloveri* in the vicinity of Lost Trails Pass (between Sula, Montana, and Gibbonsville, Idaho). Today this summit does not support many potential hosts and is probably too high in the present climate to allow *Hyalophora* to breed. The small numbers of intergrades collected near Gibbonsville could represent a remnant of a past period of hybridization.

Hybrid Zone Models and the Status of kasloensis

A consensus of recent authors believes the majority of hybrid zones are "tension zones" where character clines are maintained by an equilibrium between selection and dispersal (Barton and Hewitt, 1985, 1989; Harrison, 1990; Hewitt, 1990). An alternative view holds that hybrid zones are maintained by heterozygote advantage in ecologically disturbed or marginal habitats (Moore, 1977). Advocates of the tension-zone model assert that the typical structure of hybrid zones—long, narrow bands of coincident character clines—are unlikely to be maintained by ecological superiority for so many seemingly unrelated loci. The *kasloensis* zone exhibits the hybrid unfitness typical of a tension zone, and the fact that all taxa of *Hyalophora* are ecological generalists further argues against the ecological superiority model.

The *kasloensis* zone would appear to be one of widest recorded hybrid zones (Barton and Hewitt, 1985:table 1). Width of the zone from Kooskia, Idaho, to near Helena, Montana, is nearly 300 km, about six times the width of the Sierra Nevada *Hyalophora* hybrid zone. Zone width is directly related to dispersal potential, and Barton and Hewitt (1985) ranked the Sierra Nevada zone among recorded maxima for both parameters, and exceeded only by those of two avian hybrid zones. Regional topography, ecological features, and historical factors also determine zone structure. Density of *Hyalophora* decreases west to east, probably in response to the rainshadow effect of the Bitterroots, and consequently gene exchange with *H. c. gloveri* at present may be restricted. To the north, the Canadian Rockies effectively isolate the two populations. Such a reduction of gene flow from one side would likely have the effect of broadening the zone; this effect is indicated in the broad, gradual intergradation into the *H. euryalus* phenotype to the west and the more abrupt transition into the *H. c. gloveri* phenotype to the east.

The reduced reproductive fitness in interpopulation crosses within *kasloensis* suggests strong genetic differentiation among the source populations used in these experimental crosses. Interpopulation incompatibility is not known for either *H. euryalus* or in *H. c. gloveri* (Collins, 1984). The origin of reproductive incompatibility within *kasloensis* relates directly to a model describing genetic differentiation of isolated populations within a species and subsequent hybridization upon range expansion (Barton and Hewitt, 1989; Hewitt, 1989, 1990, 1993). This process is most likely to occur during periods of severe environmental change when the species becomes geographically subdivided, as during the Pleistocene (Hewitt, 1993). In a heterogeneous environment, isolated demes are subject to differing selection regimes that, together with genetic drift, may produce unique, adaptive genotypes. At the end of the Pleistocene, isolated populations would expand their territory. Demes with the highest fitness would be the most successful colonizers, and would swamp out neighboring populations with less favorable gene combinations. Hybrid zones would form between these pioneer populations if heterozygotes suffered reduced fitness, and these zones might act as significant barriers to introgression (Hewitt, 1989). This barrier effect is magnified by the tendency of hybrid zones to migrate to areas of low population density (Barton and Hewitt, 1985). The formation of a mosaic of genetically distinct populations bounded by hybrid zones may determine a geographic pattern of speciation as each population undergoes further differentiation (Hewitt, 1993). Hybrid zones are evidence that allopatry is not essential for differentiation in the face of potential gene flow. Because the tension zone defines regions of local adaptive equilibria separated by adaptive valleys (the zone itself), they are comparable to Wright's (1932) shifting balance between selection on individuals within a population, and random drift and interpopulation selection (Barton and Hewitt, 1989).

A process of local fitness optimization or amelioration of incompatibility is also possible in hybrid zones. Selection might favor alleles that modify the detrimental effects of heterozygosity. Several authors have cited the disruption by recombination and gene flow from parental populations of any favorable gene combinations that might arise. This argument has been offered to explain the failure of reproductive isolation to evolve in hybrid zones (Bigelow, 1965; Barton and Hewitt, 1985; Butlin, 1989). However, Virdee and Hewitt (1994) found evidence for such a local amelioration within an orthopteran hybrid zone, and Collins (1984) hypothesized that this process had produced the fully fecund intergrade females that occur in the Sierra Nevada hybrid zone, in contrast to barren lab F_1 females when crosses were made between the parental populations bordering the zone. In these cases this process is comparatively localized and has not produced a fusion of the hybridizing populations. Such a process of amelioration seems to have occurred within the Boise hybrid zone, but to a lesser extent within *kasloensis*.

The process of isolation–differentiation–subdivision by hybrid zones might have occurred within the range of *kasloensis* in addition to the formation of the original hybrid zone upon secondary contact between *H. euryalus* and *H. columbia*. If the original contact was between *H. euryalus* and the small, dark, conifer-feeding subspecies *H. c. columbia*, this event could explain the dark coloration of adult *kasloensis*, the red coloration of the fifth instar scoli (due to hybrid disruption of the expression of red pigmentation in *H. c. columbia*), and the pattern of incompatibility seen in experimental crosses (greater isolation from *H. c. gloveri* than *H. c. columbia*). Populations currently recognized as *H. c. columbia* are probably descendants of frontier populations exploiting the colonization of deglaciated terrain by their host plant *Larix*. A subsequent hybrid zone between *kasloensis* and *H. c. gloveri* then would have been established as the latter moved northward, following the spread of their deciduous, shrubby hosts. Climatic oscillations during and after the Pleistocene may have disrupted these events by temporarily subdividing the distribution of *kasloensis* into smaller, isolated populations, some of which could have survived during glacial periods. The action of drift and selection, as outlined above, on such intrinsically genetically variable populations would increase the likelihood of differentiation. Given some degree of hybrid unfitness within newly isolated hybrid populations, selection within each to improve genetic compatibility would likely produce alternative genotypes, that in turn might be incompatible upon sympatry as a result of range expansion following glacial periods. What we now refer to as *kasloensis* might represent a mosaic of such populations, similar to the model envisioned by Hewitt (1989, 1993).

Obviously, these questions beg to be explored in more detail by means of molecular techniques. Mitochondrial DNA analysis would be especially useful in determining phylogenies among populations (Avise et al., 1992; Sperling, 1993*b*), and enzyme electrophoresis and DNA sequencing techniques could measure the extent of introgression across hybrid zones and possibly resolve the question of separate contributions by *H. c. columbia* and *H. c. gloveri* to a contact zone with *kasloensis*.

CONCLUSIONS

1. Morphometric analysis, immature phenotypes, experimental hybridization, and paleoclimate and paleoflora data all independently support the interpretation of a hybrid origin for *Hyalophora "kasloensis"* as a result of range expansion and secondary contact between *H. columbia* and *H. euryalus* following allopatric divergence during the Pleistocene. The *kasloensis* zone is very wide (300 km), possibly due to topography restricting gene exchange at present with *H. c. gloveri* to the east; more gradual intergradation with *H. euryalus* occurs to the west. Compared to other *Hyalophora* hybrid zones, experimental hybridization shows significant incompatibility between *kasloensis* and congeners in terms of fertility, embryo viability, hybrid sex ratios, and fecundity of hybrid females. In addition, interpopulation crosses within *kasloensis* show some degree of incompatibility in fertility, viability, and fecundity, but not in sex ratios of "pure" *kasloensis* broods. These findings suggest that *kasloensis* populations are genetically subdivided and conform to current models of genetic divergence and the formation of hybridizing populations in the context of Pleistocene and postglacial range changes. Molecular genetic studies are needed to determine the fine structure of the hybrid zones and to evaluate these models.

2. The hybrid zone near Boise, Idaho, is similar in geographic extent and phenotypic structure to the Sierra Nevada zone. Intergrade females are probably fully fertile, and males from this zone are genetically compatible in experimental crosses with females of *H. euryalus*, *H. c. gloveri*, and *kasloensis*. By contrast, females produced by *H. c. gloveri* × *H. euryalus* crosses are barren when source populations are widely allopatric. A process of local optimization in compatibility appears to be operating within both the Boise and Sierra Nevada hybrid zones.

3. By traditional morphological criteria the *Hyalophora* have been divided into four taxa, a scheme not congruent with either prezygotic mating behavior or with postzygotic isolation. Some hybridization occurs where different recognized taxa are sympatric. All taxa apparently share a common pheromone and mate just before dawn, although slight differences in flight season and calling time partially

isolate *H. cecropia* from *H. c. columbia* (Tuttle, 1985). The well-defined hybrid zones between *H. c. gloveri* and *H. euryalus* contrast with the blend zone between *H. c. columbia* and *H. c. gloveri*, and experimental hybridization corroborates the division of *H. columbia* into two subspecies and recognition of *H. euryalus* as a distinct species. Hybrid-like specimens are produced only occasionally in contact zones between *H. cecropia* and congeners, and experimental hybridization also supports treating this taxon as a species distinct from *H. euryalus* and *H. columbia*. The formation and persistence of hybrid zones reveals significant discontinuities in genetic cohesion, and the taxa within *Hyalophora* conform to species concepts stressing this characteristic (Templeton, 1989; Avise and Ball, 1990; Mallet, 1995) but do not conform strictly to the biological species concept based on reproductive isolation. The origin of hybrid zones and taxonomic relationships within *Hyalophora* are consistent with paleoclimate reconstructions, but a test of phylogeny and species limits must await a cladistic analysis based on independent character sets.

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